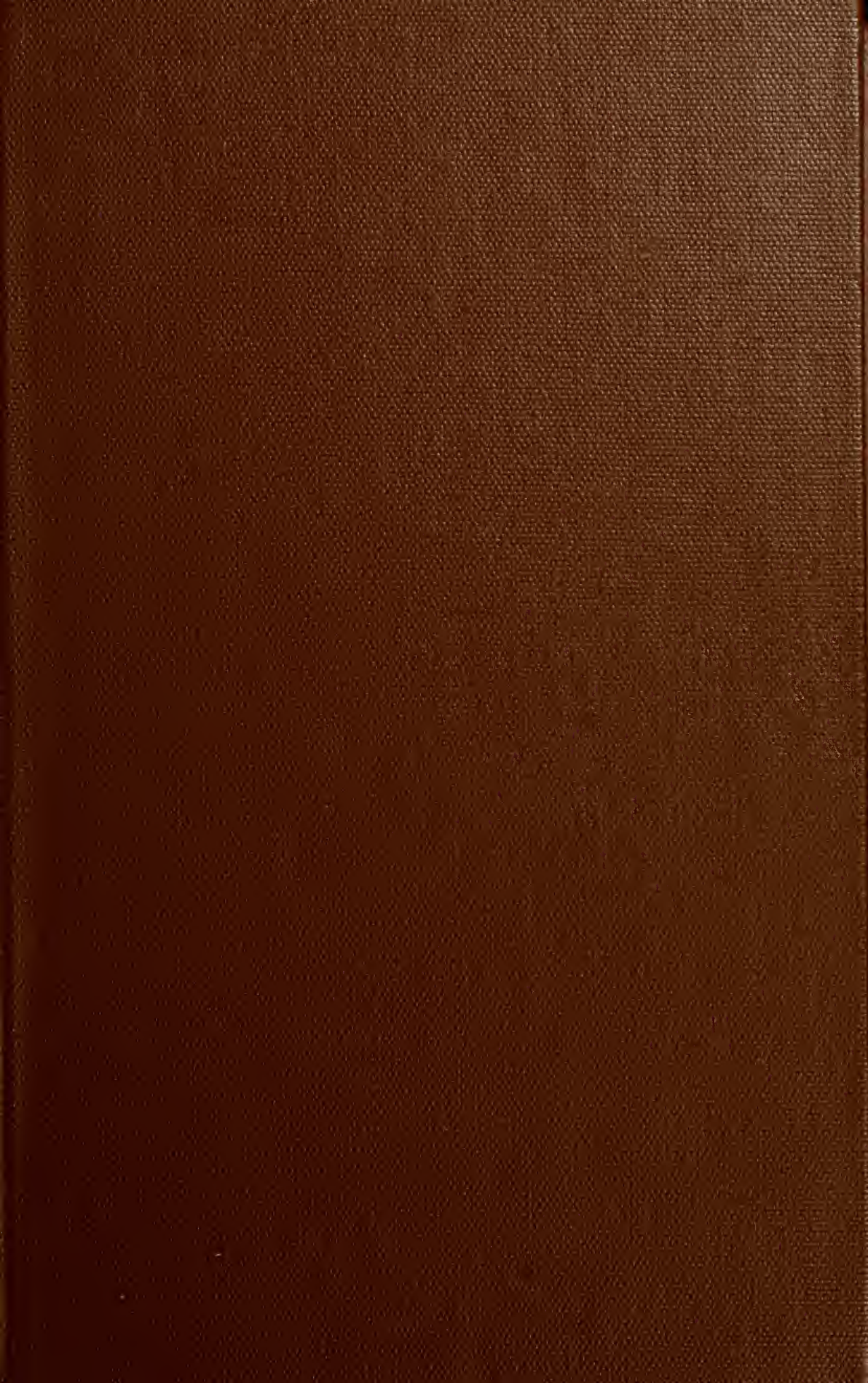




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MISCELLANEOUS
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NO. 65

**The Biology of an
Equatorial Herpetofauna
in Amazonian Ecuador**

By

William E. Duellman

UNIVERSITY OF KANSAS
LAWRENCE 1978

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THE UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

MISCELLANEOUS PUBLICATION NO. 65

August 30, 1978

The Biology of an Equatorial Herpetofauna
in Amazonian Ecuador

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Publication Supported by a Grant from the
National Science Foundation
(DEB 77-28380)

THE UNIVERSITY OF KANSAS
LAWRENCE
1978

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Editor: Linda Trueb

Miscellaneous Publication No. 65
pp. 1-352; 198 figures; 34 tables
Published August 30, 1978

MUSEUM OF NATURAL HISTORY
THE UNIVERSITY OF KANSAS
LAWRENCE, KANSAS 66045
U.S.A.

PRINTED BY
UNIVERSITY OF KANSAS PRINTING SERVICE
LAWRENCE, KANSAS

CONTENTS

INTRODUCTION	9
Acknowledgments	10
Scope of study	11
Methods	13
Reliability and Limitations of Data	13
Description of the Area	14
Physiography and Hydrography	17
Climate	19
Vegetation	22
Habitats	27
IDENTIFICATION OF SPECIES	29
Key to the Orders and Suborders of Amphibians and Reptiles	30
Key to the Caecilians	31
Key to the Salamanders	31
Key to the Frogs	31
Key to the Turtles	48
Key to the Crocodilians	49
Key to the Lizards and Amphisbaenians	49
Key to the Snakes	58
Key to the Known Tadpoles	70
SPECIES ACCOUNTS	78
Caecilians	79
Caeciliidae	79
<i>Caecilia disossea</i> Taylor	79
<i>Caecilia tentaculata</i> (Linnaeus)	79
<i>Microcaecilia albiceps</i> (Boulenger)	79
<i>Osaecilia bassleri</i> (Dunn)	80
<i>Siphonops annulatus</i> (Mikan)	80
Salamanders	80
Plethodontidae	80
<i>Bolitoglossa ecuadoriana</i> Brame and Wake	80
<i>Bolitoglossa peruviana</i> (Boulenger)	80
Frogs	82
Pipidae	82
<i>Pipa pipa</i> (Linnaeus)	82
Leptodactylidae	83
<i>Adenomera andreae</i> (Müller)	83
<i>Ceratophrys cornuta</i> (Linnaeus)	85
<i>Edalorhina perezii</i> Jiménez de la Espada	86
<i>Eleutherodactylus acuminatus</i> Shreve	86
<i>Eleutherodactylus altamazonicus</i> Barbour and Dunn	87
<i>Eleutherodactylus conspicillatus</i> (Günther)	89
<i>Eleutherodactylus croceinguinis</i> Lynch	90
<i>Eleutherodactylus diadematus</i> (Jiménez de la Espada)	91
<i>Eleutherodactylus lacrimosus</i> (Jiménez de la Espada)	92
<i>Eleutherodactylus lathanites</i> Lynch	93
<i>Eleutherodactylus martiae</i> Lynch	94
<i>Eleutherodactylus nigrovittatus</i> Andersson	96
<i>Eleutherodactylus ockendeni</i> (Boulenger)	97

<i>Eleutherodactylus orphnolaimus</i> Lynch	98
<i>Eleutherodactylus paululus</i> Lynch	98
<i>Eleutherodactylus pseudoacuminatus</i> Shreve	99
<i>Eleutherodactylus quaquaversus</i> Lynch	100
<i>Eleutherodactylus sulcatus</i> (Cope)	102
<i>Eleutherodactylus variabilis</i> Lynch	103
<i>Ischnocnema quixensis</i> (Jiménez de la Espada)	104
<i>Leptodactylus discodactylus</i> Boulenger	105
<i>Leptodactylus mystaceus</i> (Spix)	107
<i>Leptodactylus pentadactylus</i> (Laurenti)	108
<i>Leptodactylus rhodomystax</i> Boulenger	111
<i>Leptodactylus stenodema</i> Jiménez de la Espada	112
<i>Leptodactylus wagneri</i> (Peters)	112
<i>Lithodytes lineatus</i> (Schneider)	114
<i>Physalaemus petersi</i> (Jiménez de la Espada)	115
Bufonidae	116
<i>Bufo glaberrimus</i> (Günther)	116
<i>Bufo marinus</i> (Linnaeus)	117
<i>Bufo typhonius</i> (Linnaeus)	118
<i>Dendrophryniscus minutus</i> (Melin)	120
Dendrobatidae	121
<i>Colostethus marchesianus</i> (Melin)	121
<i>Colostethus sauli</i> Edwards	123
<i>Dendrobates parvulus</i> Boulenger	124
<i>Dendrobates pictus pictus</i> Duméril and Bibron	125
<i>Dendrobates quinquevittatus</i> Steindachner	125
<i>Phyllobates femoralis</i> (Boulenger)	126
Hylidae	127
<i>Hemiphractus proboscideus</i> (Jiménez de la Espada)	127
<i>Hyla alboguttata</i> Boulenger	128
<i>Hyla bifurca</i> Andersson	130
<i>Hyla boans</i> (Linnaeus)	131
<i>Hyla bokermanni</i> Goin	133
<i>Hyla brevifrons</i> Duellman and Crump	135
<i>Hyla calcarata</i> Troschel	137
<i>Hyla cruentomma</i> Duellman	139
<i>Hyla fasciata</i> Günther	140
<i>Hyla favosa</i> Cope	142
<i>Hyla funerea</i> (Cope)	143
<i>Hyla garbei</i> (Miranda-Ribeiro)	144
<i>Hyla geographica</i> Spix	146
<i>Hyla granosa</i> Boulenger	148
<i>Hyla lanciformis</i> (Cope)	150
<i>Hyla leucophyllata</i> (Bereis)	152
<i>Hyla marmorata</i> (Laurenti)	153
<i>Hyla minuta</i> Peters	155
<i>Hyla parviceps</i> Boulenger	156
<i>Hyla punctata</i> (Schneider)	158
<i>Hyla rhodopepla</i> Günther	159
<i>Hyla riveroi</i> Cochran and Goin	161

<i>Hyla rossalleni</i> Goin	162
<i>Hyla rubra</i> Laurenti	163
<i>Hyla sarayacuensis</i> Shreve	165
<i>Hyla triangulum</i> Günther	167
<i>Nyctimantis rugiceps</i> Boulenger	168
<i>Osteocephalus buckleyi</i> (Boulenger)	170
<i>Osteocephalus leprieurii</i> (Duméril and Bibron)	171
<i>Osteocephalus taurinus</i> Steindachner	172
<i>Phrynohyas coriacea</i> (Peters)	173
<i>Phrynohyas venulosa</i> (Laurenti)	174
<i>Phyllomedusa palliata</i> Peters	176
<i>Phyllomedusa tarsius</i> (Cope)	177
<i>Phyllomedusa tomopterna</i> (Cope)	179
<i>Phyllomedusa vaillanti</i> Boulenger	180
<i>Sphaenorhynchus carneus</i> (Cope)	181
<i>Sphaenorhynchus eurhostus</i> Rivero	182
Centrolenidae	183
<i>Centrolenella midas</i> Lynch and Duellman	183
<i>Centrolenella munozeorum</i> Lynch and Duellman	184
<i>Centrolenella resplendens</i> Lynch and Duellman	185
Ranidae	186
<i>Rana palmipes</i> Spix	186
Microhylidae	187
<i>Chiasmocleis anatis</i> Walker and Duellman	187
<i>Chiasmocleis bassleri</i> Dunn	188
<i>Chiasmocleis ventrimaculata</i> (Andersson)	189
<i>Ctenophryne geayi</i> Mocquard	190
<i>Hamptophryne boliviana</i> (Parker)	190
<i>Syncope antenori</i> Walker	192
Turtles	192
Cheliidae	192
<i>Chelus fimbriatus</i> (Schneider)	192
<i>Mesoclemmys gibba</i> (Schweigger)	192
<i>Phrynops geoffroanus tuberosus</i> (Peters)	193
<i>Platemys platycephala</i> (Schneider)	193
Kinosternidae	193
<i>Kinosternon scorpioides</i> (Linnaeus)	193
Testudinidae	194
<i>Geochelone denticulata</i> (Linnaeus)	194
Crocodylians	194
Crocodylidae	194
<i>Caiman crocodilus crocodilus</i> (Linnaeus)	194
<i>Paleosuchus trigonatus</i> (Schneider)	195
Lizards	195
Gekkonidae	195
<i>Gonatodes concinnatus</i> (O'Shaughnessy)	195
<i>Pseudogonatodes guianensis</i> Parker	196
<i>Thecadactylus rapicauda</i> (Houttuyn)	197
Iguanidae	198
<i>Anolis chrysolepis scypheus</i> Cope	198

<i>Anolis fuscoauratus fuscoauratus</i> D'Orbigny	199
<i>Anolis ortonii</i> Cope	200
<i>Anolis punctatus boulengeri</i> O'Shaughnessy	201
<i>Anolis trachyderma</i> Cope	201
<i>Anolis transversalis</i> Duméril	202
<i>Enyaliodes cofanorum</i> Duellman	203
<i>Enyaliodes laticeps festae</i> Peracca	204
<i>Plica umbra ochrocollaris</i> (Spix)	206
<i>Polychrus marmoratus</i> (Linnaeus)	207
<i>Uracentron flaviceps</i> (Guichenot)	208
Scincidae	208
<i>Mabuya mabouya</i> (Lacépède)	208
Teiidae	209
<i>Alopoglossus atriventris</i> Duellman	209
<i>Alopoglossus copii</i> Boulenger	210
<i>Ameiva ameiva petersii</i> Cope	210
<i>Arthrosaura reticulata</i> (O'Shaughnessy)	213
<i>Bachia trinasale trinasale</i> (Cope)	213
<i>Dracaena guianensis</i> Daudin	214
<i>Iphisa elegans</i> Gray	215
<i>Kentropyx pelviceps</i> Cope	215
<i>Leposoma parietale</i> (Cope)	217
<i>Neusticurus ecleopus</i> Cope	218
<i>Prionodactylus argulus</i> (Peters)	220
<i>Prionodactylus manicatus</i> (O'Shaughnessy)	221
<i>Ptychoglossus brevifrontalis</i> Boulenger	222
<i>Tupinambis teguixin</i> (Linnaeus)	223
Amphisbaenians	224
Amphisbaenidae	224
<i>Amphisbaena fuliginosa</i> Linnaeus	224
Snakes	224
Aniliidae	224
<i>Anilius scytale</i> (Linnaeus)	224
Boidae	225
<i>Boa constrictor constrictor</i> Linnaeus	225
<i>Corallus caninus</i> (Linnaeus)	225
<i>Corallus enydris enydris</i> (Linnaeus)	226
<i>Epicrates cenchria cenchria</i> (Linnaeus)	226
<i>Eunectes murinus murinus</i> (Linnaeus)	227
Colubridae	227
<i>Atractus elaps</i> (Günther)	227
<i>Atractus major</i> Boulenger	229
<i>Attractus occipitoalbus</i> (Jan)	230
<i>Chironius carinatus</i> (Linnaeus)	231
<i>Chironius fuscus</i> (Linnaeus)	232
<i>Chironius multiventris</i> Schmidt and Walker	233
<i>Chironius scurrulus</i> (Wagler)	234
<i>Clelia clelia clelia</i> (Daudin)	235
<i>Dendrophidion dendrophis</i> (Schlegel)	236
<i>Dipsas catesbyi</i> (Santzen)	237

<i>Dipsas indica ecuadorensis</i> Peters	238
<i>Dipsas pavonina</i> Schlegel	239
<i>Drepanoides anomalus</i> (Jan)	240
<i>Drymobius rhombifer</i> (Günther)	240
<i>Drymoluber dichrous</i> (Peters)	241
<i>Erythrolamprus aesculapii aesculapii</i> (Linnaeus)	242
<i>Helicops angulatus</i> (Linnaeus)	242
<i>Helicops petersi</i> Rossman	243
<i>Imantodes cenchoa cenchoa</i> (Linnaeus)	244
<i>Imantodes lentiferus</i> (Cope)	245
<i>Leimadophis reginae</i> (Linnaeus)	246
<i>Leimadophis</i> sp.	247
<i>Leptodeira annulata annulata</i> (Linnaeus)	247
<i>Leptophis ahuetulla nigromarginatus</i> (Günther)	249
<i>Liophis cobella</i> (Linnaeus)	250
<i>Ninia hudsoni</i> Parker	250
<i>Oxybelis argenteus</i> (Daudin)	251
<i>Oxyrhopus formosus</i> (Wied)	253
<i>Oxyrhopus melanogenys</i> (Tschudi)	253
<i>Oxyrhopus petola digitalis</i> (Reuss)	254
<i>Pseudoboa coronata</i> Schneider	255
<i>Pseustes sulphureus sulphureus</i> (Wagler)	255
<i>Rhadinaea brevirostris</i> (Peters)	255
<i>Siphlophis cervinus</i> (Laurenti)	256
<i>Tantilla melanocephala melanocephala</i> (Linnaeus)	256
<i>Tripanurgos compressus</i> (Daudin)	258
<i>Xenodon severus</i> (Linnaeus)	258
<i>Xenopholis scalaris</i> (Wucherer)	260
Elapidae	260
<i>Leptomicrurus narduccii</i> (Jan)	260
<i>Micrurus langsdorffi langsdorffi</i> Wagler	260
<i>Micrurus lemniscatus helleri</i> Schmidt and Schmidt	261
<i>Micrurus spixii obscurus</i> (Jan)	261
<i>Micrurus surinamensis surinamensis</i> (Cuvier)	262
Crotalidae	262
<i>Bothrops atrox</i> (Linnaeus)	262
<i>Bothrops bilineatus smaragdinus</i> Hoge	264
<i>Bothrops castelnaudi</i> Duméril, Bibron and Duméril	264
<i>Lachesis muta muta</i> (Linnaeus)	265
REPRODUCTIVE BIOLOGY	265
Annual Reproductive Patterns	266
Anurans	266
Lizards	270
Snakes	271
Fecundity	271
Anurans	272
Lizards	273
Snakes	276
Reproductive Strategies	280
Anurans	280

Lizards	285
Snakes	287
Discussion	288
Reproduction in Other Groups	288
Reproductive Potential	288
General Conclusions	289
Seasonal Versus Aseasonal Environments	289
COMMUNITY STRUCTURE	291
Habitat Analysis	294
Primary Forest	298
Secondary Forest	310
Clearings	311
Diel Activity	312
Diet and Feeding	313
Size Ratios	314
Tadpoles	315
Anuran Mating Calls	318
Niche Dimensions	319
Species Diversity	323
Discussion	327
Seasonal Versus Aseasonal Environments	330
BIOGEOGRAPHY	331
Distribution of the Herpetofauna	331
Origin of the Herpetofauna	335
Tertiary and Quaternary History of the Amazonian Biota	336
Evolution of the Herpetofaunal Community	338
EPILOGUE	339
RESUMEN	341
LITERATURE CITED	345

PLATES FOLLOW PAGE 192

INTRODUCTION

Civilized man has walked on the moon and is carrying out exploratory probes of outer space; yet there remain on earth two nearly unknown ecosystems—the depths of the oceans and the lowland tropical rainforest. Technological problems limit the exploration of oceans, but the tropical lowlands? Is the “foreboding jungle,” to which the exaggerated writings of travelers and adventurers all-too-often refer, beyond the limits of modern technology?

In the Nineteenth Century a few naturalists ventured into the Amazon Basin in South America. The vast collections and provocative writings of Henry W. Bates, Alexander von Humboldt, Richard Spruce, and Alfred R. Wallace should have provided the impetus for continued and intensive exploration and study. Africa, with its relatively small Congo Basin, was the “dark continent” to be explored, colonized, and exploited, whereas South America, which so richly deserves the appellation given to Africa, languished. Although the short-lived “rubber boom” late in the last century left an opera house in Manáus, the Amazon Basin remained a biological *tierra incognita*.

Now the Amazon Basin is being exploited—before it has been adequately explored and studied. Human population pressure coupled with food and energy shortages seem to make it “practical” to settle the vast region, construct roads, clear the forests, cultivate the soil, and drill for oil. The lateritic soil is leached and eroded after two or three crops; the rivers are polluted; and we are losing forever a part of the world’s biota. For the most part biologists are still ignorant of the fauna and flora of the Amazon Basin and have little accurate conception of the ecology of the rainforest. Ironically, the Biome Study Committee of the International Biological Program never succeeded in initiating a study of the tropical rainforest.

Today many biologists are concerned primarily with theoretical aspects of population biology, ecology, and evolution. Models of species diversity, niche breadth and overlap, resource partitioning, competition, predator-prey, and r and K selection abound in the literature. But how do these models apply to the tropics? Where and how can they be tested? Although inferences frequently are made in the literature, base line data are wanting in most cases.

The present report is an attempt to present base line data and preliminary interpretations. Hopefully, they will provide future investigators with the information and impetus for more intensive and varied ecological and population studies, which in turn will furnish the bases for testing models. This report concerns the amphibians and reptiles of Santa Cecilia, a small area in the upper Amazon Basin. It deals with the amphibians and reptiles for two reasons. First, I am a herpetologist and am most knowledgeable about those groups. Second, amphibians and reptiles are ideal organisms for faunal study in the tropics. They are closely tied to the environment, usually are independent of given species of plants, and are sufficiently numerous and well enough known to be studied feasibly. The choice of the study area was completely fortuitous.

During the past ten years numerous publications dealing with the herpetofauna of the Santa Cecilia region have appeared. Many of these have been descriptions of new species: *Eleutherodactylus croceinguinis* and *variabilis* (Lynch, 1968); *E. orphnolaimus* (Lynch, 1970); *E. martiae*, *paululus*, and *quaquaversus* (Lynch, 1974); *E. lanthanites* (Lynch, 1975); *Colostethus sauli* (Edwards, 1974); *Hyla brevifrons* (Duellman and Crump, 1974); *Hyla cruentomma* (Duellman, 1972a); *Centrolenella midas*, *munozorum*, and *resplendens* (Lynch and Duellman, 1973); *Chiasmo-*

cleis anatypes (Walker and Duellman, 1974); *Syncope antenori* (Walker, 1973); *Enyalioides cofanorum* and *Alopoglossus atriventris* (Duellman, 1973c); and *Heliocops petersi* (Rossman, 1976). Other papers deal with the taxonomic status of various taxa: *Phrynohyas coriacea* (Duellman, 1968); *Hyla funerea* (Duellman, 1971b); *Hyla garbei* (Duellman, 1970a); *Hyla rhodopepla* (Duellman, 1972c); *Hyla punctata*, *rossalleni*, *leucophyllata* group and *Sphaenorhynchus carneus* (Duellman, 1974a); and Amazonian *Phyllomedusa* (Duellman, 1974b). Material from Santa Cecilia has been used in the following systematic reviews: *Hyla geographica* group (Duellman, 1973b); *Hyla parviceps* group (Duellman and Crump, 1974); *Hyla rostrata* group (Duellman, 1972b); *Osteocephalus* (Trueb and Duellman, 1971); *Hemiphractus* (Trueb, 1974); *Nyctimantis* (Duellman and Trueb, 1976); and Ecuadorian caecilians (Taylor and Peters, 1974). Fitch (1968) reported on body temperatures of several species of lizards. Crump (1974) provided a thorough analysis of reproductive strategies in the anurans, and Simmons (1975) analyzed the female reproductive cycle in *Ameiva ameiva*.

ACKNOWLEDGMENTS

Field studies were initiated at Santa Cecilia primarily because of the existence of a base camp, "Muñozlandia." Our work there was made possible by Ing. Ildefonso Muñoz B., who provided housing and a laboratory. He and his family made it possible for us to devote full time to biological studies while enjoying rustic, but comfortable, accommodations in the jungle. For their gracious hospitality, which included numerous *fiestas* and *despedidas*, I extend my sincere *muchísimas gracias* to the Muñoz family.

I am grateful to the personnel of Gulf Oil Ecuador and Texaco Petroleum Company, Ecuador, for providing air trans-

portation between Quito and the Oriente and also for many other courtesies. Ecuadorian army personnel stationed at Santa Cecilia aided us in many ways; I am especially indebted to Colonel Ramirez. Our work in Quito was greatly facilitated by personnel at the Universidad Católica del Ecuador; I especially thank Father Gustavo Maldonado, Dra. Olga Herrera de MacBryde, and the late Francisco León.

Muñozlandia was "discovered" by Charles M. Fugler, formerly of Auburn University. I will be forever grateful to Fugler for his telephone call to me in October 1966 in which he suggested Santa Cecilia as a study site.

The data and specimens upon which this report is based were accumulated mostly by field parties from The University of Kansas. I thank each person for their contribution and list them in descending order of the amount of time spent at Santa Cecilia: Martha L. Crump, John E. Simmons, Linda Trueb, Stephen R. Edwards, James W. Wad-dick, Thomas H. Fritts, Charles F. Walker, John D. Lynch, Henry S. Fitch, Abraham Goldgewicht K., Werner C. A. Bokermann, Joseph T. Collins, Arthur C. Echternacht, and Robert W. Henderson. In addition to these persons, all of whom were primarily concerned with studies on the herpetofauna, I am indebted to Philip S. Humphrey, Stephen R. Humphrey, Frank B. Cross, Gerald R. Smith, and especially William G. Saul for their contributions made incidental to their studies on the birds and fishes. Charles M. Fugler, George Key, and Terry D. Schwaner collected amphibians and reptiles at Santa Cecilia; their specimens were deposited at Auburn University Museum and the Museum of Comparative Zoology at Harvard University. I am indebted to Schwaner for field notes and photographs and to Robert H. Mount and Ernest E. Williams for the loan of specimens. Charles F. Walker kindly made available material that he collected and deposited in the University of Mich-

igan Museum of Zoology. Ronn Altig, Mississippi State University, collected at Santa Cecilia in 1973-1975; I am grateful to him for making material available to me.

Some of the limited information provided herein on the geology and vegetation was derived in part from information provided by Richard Govett of the Texaco Petroleum Company, John Dwyer of the Missouri Botanical Garden, and Bruce MacBryde, formerly of the Universidad Católica del Ecuador. I was fortunate in being able to spend time in the field with each of them.

The identification of the material collected at Santa Cecilia has been a long and arduous task that required visits to many museums; I am grateful to curators of these collections in the United States, Europe, and South America for their hospitality and provision of working space. Specimens of some groups have been studied by others, who have provided me with identifications and insights into the systematics of these groups. Thus, I am grateful to Edward H. Taylor (caecilians), Federico Medem (pleurodire turtles), Charles W. Myers (*Leimadophis* and *Rhadinaea*), Douglas A. Rossman (*Helicops*), W. Ronald Heyer (*Leptodactylus*), and Charles F. Walker (microhylids), and especially John D. Lynch for his efforts on the difficult genus *Eleutherodactylus*. I am extremely appreciative of the aid provided by the late James A. Peters, who on many occasions shared with me his extensive knowledge of the Ecuadorian herpetofauna.

The field studies were variously supported by the Herpetological Research Fund, F. William Saul Fund, and the Watkins Museum of Natural History Grants, all of The University of Kansas. Crump's field work in 1971-72 was supported by the National Science Foundation (GB-29557). Visits to European museums were made possible by a grant from the Penrose Fund of the American Philosophical Society (No. 5063), and

part of the laboratory work was supported by a grant from the General Research Fund, The University of Kansas. A grant from the National Science Foundation (GB-35483) made possible the completion of the research.

During the preparation of this report I have been assisted by Jan Caldwell, Albert Fisher, Julian C. Lee, John E. Simmons, and especially Martha L. Crump. I sincerely thank them for their careful and extensive work. I am indebted to James R. Dixon and John D. Lynch for critically reviewing the taxonomic accounts and to Martha L. Crump for her provocative discussions and critical review of the manuscript. I am grateful to Juan R. León and Jaime E. Péfaur for translating the keys and summary into Spanish. Many of the photographs in this report were taken by Crump and Simmons; I thank them for permission to reproduce the photographs, and I am grateful to Simmons for his painstaking work in the darkroom.

Indeed I have been fortunate in having the opportunities to undertake this research and in having the cooperation of so many associates. But my most cherished fortune is my wife, Linda Trueb. She accompanied me on four trips to Santa Cecilia, assiduously worked in the field, and collaborated in several preliminary reports. She has provided many ideas for the organization, analysis, and interpretation of the data, and she has critically read the entire manuscript. But her major contributions to this report are her illustrations, the usefulness of which shall, I fear, long outlive my less colorful prose. Hers has been a labor of love, which I can never repay in kind.

SCOPE OF STUDY

The material presented herein is the result of 48 man months of field work at Santa Cecilia on the Río Aguarico, Provincia Napo, Ecuador, plus smaller collections of specimens and data from four nearby localities along the Río

TABLE 1.—Taxonomic Summary of the Herpetofauna of the Upper Río Aguarico, Ecuador.
(The numbers given first are for the entire area; numbers in parentheses
are for Santa Cecilia only)

ORDER: Family	Genera	Species	Specimens
GYMNOPHIONA			
Caeciliidae	4 (2)	5 (3)	65 (22)
CAUDATA			
Plethodontidae	1 (1)	2 (2)	122 (22)
ANURA			
Pipidae	1 (1)	1 (1)	8 (8)
Leptodactylidae	8 (8)	28 (25)	2109 (1602)
Bufonidae	2 (2)	4 (4)	473 (456)
Dendrobatidae	3 (3)	6 (5)	579 (526)
Hylidae	7 (7)	38 (37)	3060 (2859)
Centrolenidae	1 (1)	3 (3)	27 (20)
Ranidae	1 (1)	1 (1)	98 (97)
Microhylidae	4 (3)	6 (5)	111 (97)
TESTUDINES			
Cheliidae	4 (4)	4 (4)	18 (17)
Kinosternidae	1 (1)	1 (1)	9 (9)
Testudinidae	1 (1)	1 (1)	7 (3)
CROCODYLIA			
Crocodylidae	2 (2)	2 (2)	16 (13)
SAURIA			
Gekkonidae	3 (3)	3 (3)	62 (47)
Iguanidae	5 (5)	11 (10)	849 (749)
Scincidae	1 (1)	1 (1)	44 (35)
Teiidae	12 (12)	14 (13)	823 (724)
AMPHISBAENIA			
Amphisbaenidae	1 (1)	1 (1)	6 (3)
SERPENTES			
Aniliidae	1 (1)	1 (1)	7 (3)
Boidae	4 (4)	5 (5)	21 (19)
Colubridae	26 (24)	38 (36)	459 (384)
Elapidae	2 (2)	5 (5)	18 (15)
Crotalidae	2 (2)	4 (4)	41 (35)
TOTALS	97 (92)	185 (173)	9035 (7765)

Aguarico. The area that was studied at Santa Cecilia consisted of about 3 square kilometers. During the course of the field work, efforts were made to collect series of each species from every month of the year and to obtain data on the microhabitat, activity, and life history of each species. As a result of the field work, 9035 specimens (+292 lots of tadpoles) representing 185 species were obtained; 7765 specimens (+288 lots of tadpoles) of 173 species are from Santa Cecilia (Table 1). These specimens and their accompanying data form the documentation for one of the richest herpetofaunas known from any one area in the world.

The bulk of this report is descriptive. Many of the species have never been

described in detail, and most never have been illustrated. I present descriptions of the animals based on living colors and illustrations of most of the species. The tadpoles of 46 frogs are described. As an aid to the identification of species of amphibians and reptiles in the upper Amazon Basin, illustrated keys are offered in English and Spanish.

In attempting to analyze reproductive patterns and strategies I have summarized the data for all of the species and evaluated the data with respect to size of the animal, clutch size, mode of reproduction, and seasonality.

Perhaps the most interesting aspect of this report is the interpretation of the data with respect to the co-existence of

so many species. Thus, in viewing resource utilization I have analyzed data on general habitat, structural habitat, diel and seasonal activity, and food. In concert with information on phylogenetic relationships and distributions of the component species, the ecological and reproductive data provide a basis from which an hypothesis on the evolution of this large tropical community is formulated.

METHODS

All specimens were preserved in 10 percent formalin and subsequently stored in 70 percent ethanol, except tadpoles which were stored in formalin. Colors in life were noted in the field, and series of colored transparencies were taken. In the laboratory, animals were measured to the nearest millimeter. Gonads were examined only in females. Ovarian eggs were counted individually or in cases of frogs having several thousand eggs, a set volume was counted, and the total number was calculated on the basis of volume. Eggs were measured to the nearest 0.1 mm. Stomach contents were analyzed in 25 individuals (or as many as possible when 25 were not available) of each species. Prey items were identified to as small a taxonomic category as possible in vertebrates and to order in arthropods, save for gryllotalpids and blattids, which were distinguished from other orthopterans. The numbers of each kind of prey in a given stomach were noted, and the percentage volume of each kind was estimated.

Climatic data at Santa Cecilia were obtained from a rain gauge in a clearing and a maximum-minimum thermometer kept in a thatch-roofed building. Daily readings were taken at about 0800 hr each day. Because of the richness and complexity of the flora, no attempt was made at a floristic analysis; the vegetation was studied only in a structural context. Plant collections from Santa Cecilia exist in the Shaw Herbarium of the Missouri Botanical Garden in St. Louis

and in the Herbarium, Universidad Católica del Ecuador in Quito.

RELIABILITY AND LIMITATIONS OF DATA

Ideally in a study of this sort, all of the data would be collected in precisely the same manner. Furthermore, equal amounts of time would be spent sampling different habitats throughout the year. However, such was not the case at Santa Cecilia, where our early field work (1966-1967) was devoted primarily to a faunal survey. Although data on the microhabitats and life histories of the species were obtained then, the data were not recorded in the coded framework utilized in the later field studies. Consequently, the amount of useable ecological data usually is less than the numbers of specimens indicate.

The greatest inconsistency in the data base is the unequal sampling throughout the year. Although one field party worked continuously at Santa Cecilia from June 1971 to July 1972, the other field parties were there for shorter periods of time and usually in June, July, and August. Thus, the number of man days of field work in July (309) is far greater than in many other months, especially January (39) and December (44). There is a corresponding disparity in the number of species and specimens from different months (Fig. 1). Consequently, conclusions concerning activity or reproduction of a given species are biased by the few data from some months (January and December especially). Accordingly, if some females of a given species are gravid in every month, except January and December, months from which only one or two non-gravid females are available, I have been inclined to state that the species breeds throughout the year. On the other hand, the absence of gravid females in July is considered to be valid.

Although field studies were conducted throughout the year, the collecting of tadpoles was sporadic. Consequently,

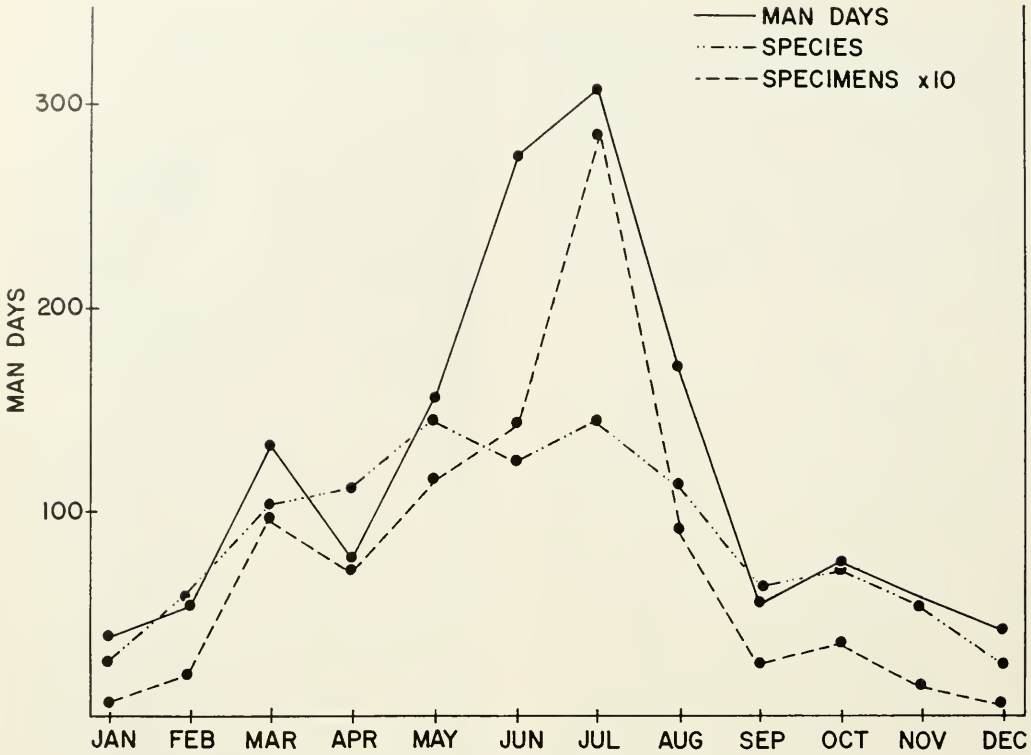


FIG. 1.—Comparative monthly rates of collecting effort and results at Santa Cecilia.

data on occurrence of tadpoles was used only in a positive way—*i.e.*, absence of data on tadpoles in a given habitat or at a time of the year was not considered to be reliable.

DESCRIPTION OF THE AREA

The Amazon Basin, with an area of about 6,000,000 square kilometers, straddles the equator and extends from the base of the Andes about 3000 kilometers eastward to the Atlantic Ocean. With the exception of some low hills and plateaus, the elevation diminishes gradually from about 500 meters at the base of the Andes to sea level at the mouth of the Amazon. Although Ecuador is a small country with a coastline on the Pacific Ocean and with the Andes bisecting the country from north to south, approximately one-third of the country lies in Amazon Basin (Fig. 2), a region referred to locally as the Oriente. The major

river in the Oriente is the Río Napo, which flows southeastward to join the Río Marañón near Iquitos, Perú, and form the Río Solimões. The latter flows eastward to Manáus, Brasil, where it is joined by the Río Negro to form the great Río Amazonas.

One of the major tributaries of the Río Napo is the Río Aguarico; the latter is formed by the confluence of the Río Cofanes and the Río Chingual, both of which drain the eastern face of the Andes in northern Ecuador. The confluence is at an elevation of 600 meters; from this point the Río Aguarico flows rapidly in a boulder-strewn bed to a point below Santa Cecilia (340 m). Throughout the remaining two-thirds of the length of the river, it is broad, primarily silt-bottomed, and drops to an elevation of about 200 meters at its confluence with the Río Napo.

Geologically the region of the upper

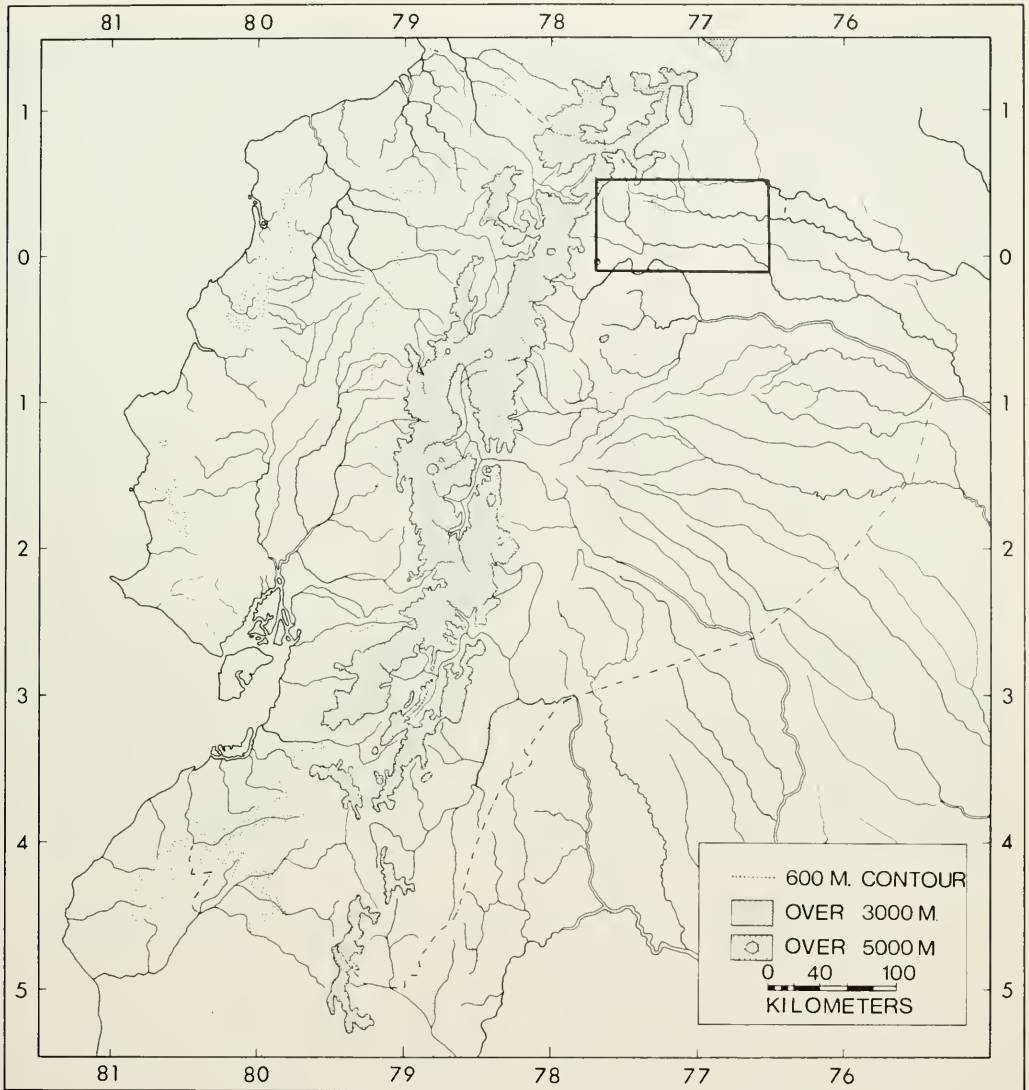


FIG. 2.—Map of Ecuador showing location of the upper Río Aguarico area.

Río Aguarico consists of deep Tertiary alluvial deposits (2500-3000 m) above Cretaceous marine sandstones (Tschopp, 1953; Harrington, 1962). Following the terminology of Beek and Bramao (1969), two principal soil types occur in the region. Closest to the Andes and continuing eastward in the well-drained areas are reddish brown laterites, whereas red-yellow podzols occur in poorly drained areas removed from the Andes. Pale yellow latosols and low humic grey

soils occur in extreme eastern Ecuador, but apparently these either are absent or inconspicuous in the region studied. The beaches along the Río Aguarico are quartz sand or river pebbles. The average size of the latter varies from about 30 cm near the base of the Andes to about 10 cm at Santa Cecilia.

Whereas the primary study area consisted of about 3 square kilometers at Santa Cecilia, four other sites along the Río Aguarico were included as secondary

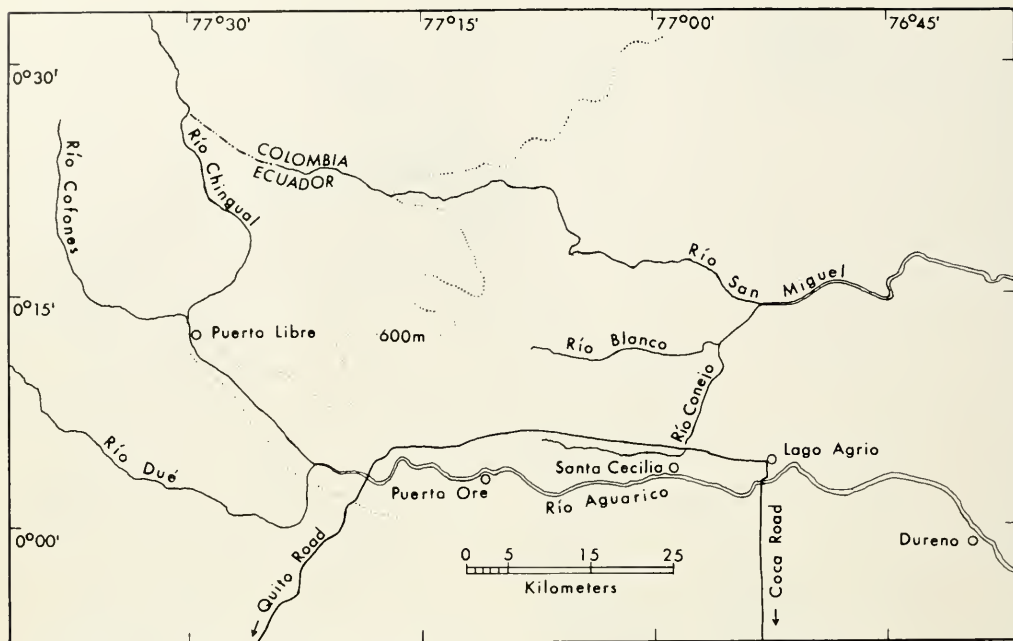


FIG. 3.—Map of the upper Río Aguarico showing location of study sites.

study areas; together these encompassed an airline distance of about 85 kilometers and an elevational range of 320-570 meters (Fig. 3). The five sites are described below:

Dureno.— $00^{\circ}02'S$, $76^{\circ}30'W$; 320 m. This small Cofan Indian village is on the south bank of the Río Aguarico. A few hectares around the village were cultivated; elsewhere there was primary forest (1967).

Lago Agrio.— $00^{\circ}03'N$, $76^{\circ}53'W$; 340 m. This is now the major petroleum center in the Oriente of Ecuador with a large airfield, refinery, and town of about 2500 people. When field work was done there (1969), the area was virgin primary forest. This site should not be confused with a small lake by the same name about 3 kilometers to the northwest.

Puerto Libre.— $00^{\circ}12'N$, $77^{\circ}29'W$; 570 m. This is an intermittent placer mining camp with a grass airstrip situated in a narrow valley at the base of the Andean foothills. In 1968 there was secondary forest in the immediate vicinity of the camp; elsewhere the area was covered by primary forest.

Puerto Ore.— $00^{\circ}03'N$, $77^{\circ}11'W$; 420 m. This was a temporary placer mining camp on the south bank of the Río Aguarico. The area mostly supported primary forest (1968).

Santa Cecilia.— $00^{\circ}03'N$; $76^{\circ}59'W$; 340 m. Prior to 1965 this was a small Quechua Indian village scattered along the north bank of the Río Aguarico. In 1965, Texaco-Gulf established a petroleum exploration camp and built an airstrip. When field studies were initiated in November 1966 most of the area was covered by primary forest (Fig. 4). The exceptions were the clearings for the airfield, exploration camp, and the two-hectare compound "Muñozlandia", which served as our base camp. Adjacent to the village of Santa Cecilia were some fields of *plátanos* and *yuca*. All human habitation and disturbance were between the Río Aguarico and the much smaller Río Conejo lying 1-2 kilometers to the north. The Río Conejo flows northward into the Río San Miguel, a tributary of the Río Putumayo, which is a large river flowing eastward into the Río Solimões. Beginning in 1966 each succeeding year

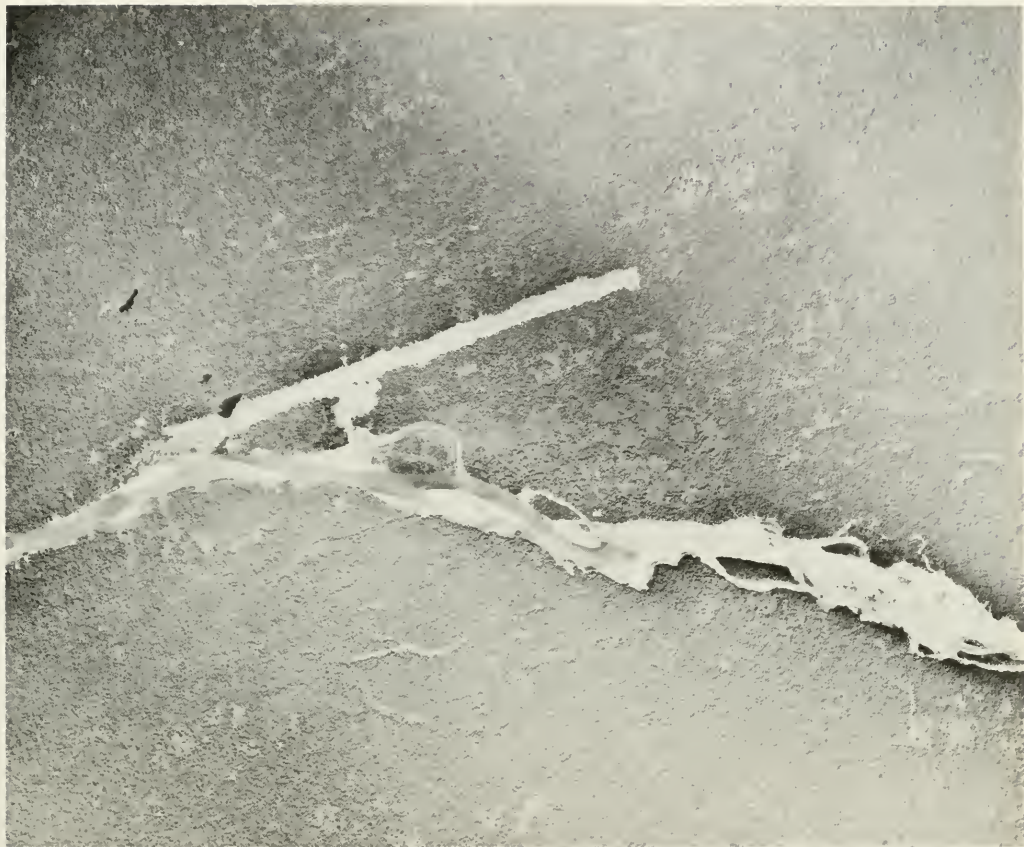


FIG. 4.—Aerial photograph of the Río Aguarico encompassing the village of Santa Cecilia on the north bank of the river at the left edge of the picture and the airstrip (diagonal clearing in middle of picture). The darker irregular tones are forest; the pale areas are swamps dominated by *Heliconia*. Photographed 2 February 1966 (courtesy of U.S. Air Force).

brought more people into Santa Cecilia and more destruction of the forest, so that by 1971 many farms of 50 or more hectares had been hacked out of the forest. In October 1971 the road between Quito and Lago Agrio was completed; the oil companies moved to Lago Agrio, and the Ecuadorian army took over the oil camp (Fig. 5). With the completion of the road, most of the families that had been living on the river bank moved to the road; in so doing, they abandoned their homes and cultivated areas. Thus, Santa Cecilia, as a village no longer exists. Many of its former inhabitants now own 50-hectare homesteads along the road.

Unless specified otherwise, the infor-

mation in the following sections pertains only to the area of Santa Cecilia.

PHYSIOGRAPHY AND HYDROGRAPHY

The terrain is generally flat with numerous small streams and depressions; the total relief is about 20 meters. The airstrip occupies a narrow ridge between the Río Aguarico and Río Conejo. From Muñozlandia eastward the ridge gradually diminishes to the Río Aguarico, but upstream there is a bluff along the river. The higher ground encompasses most of the area between the Río Conejo and the Río Aguarico west of the airstrip.

The Río Aguarico is a "white water" river with a width of about 100 meters at Santa Cecilia. According to Saul

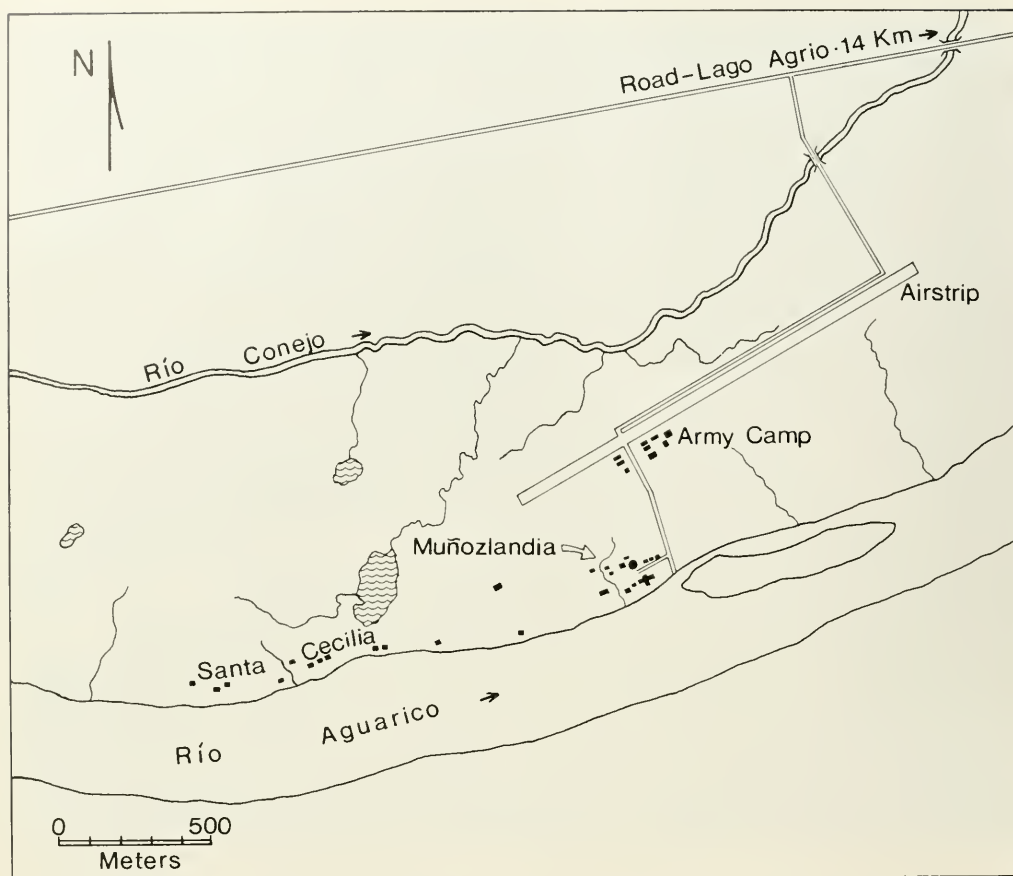


FIG. 5.—Map of the study area at Santa Cecilia. All work was done between the Río Aguarico and the Río Conejo and from the small lake at the extreme left to the eastern end of the airstrip.

(1975), the velocity frequently exceeds 2.0 meters per second, and the surface temperature varies between 18° and 20° C. Water level fluctuations of about 5 meters were common and mostly associated with heavy rains on the Andean slopes. At times of high water, the size of the island at Santa Cecilia was markedly reduced, and local residents claimed to have seen the entire island covered with water. In contrast, at times of low water a broad, boulder and silt bar connects the western end of the island with the north bank of the river (Fig. 6), resulting in an extensive backwater lagoon on the north side of the island.

The Río Conejo is a shallow (up to 2 meters), meandering stream about 6

meters in width. In undisturbed areas the river is concealed by the forest. The velocity is 0.3-0.6 meters per second, and the surface temperatures are 22-23° C. (Saul, 1975). Other streams in the area are small (< 3 meters wide) and shallow. They vary in gradient from some spring-fed rivulets that descend over rock and gravel from the ridge to the Río Aguarico to silt-bottomed streams draining lakes and swamps.

Two permanent lakes are present in the area. The southern lake is the largest ($\pm 150 \times 300$ m), whereas the northern is about 100 m in diameter. Both lakes are deep; actual depths are unknown but exceed 10 m. Originally these eutrophic lakes were bordered by



FIG. 6.—The Río Aguarico, looking downstream from Muñozlandia. In the foreground is the bar extending to the island at a time of low water.

primary forest (Fig. 7). Surface temperatures of the southern lake fluctuate daily from 23.8° to 27.8° C (Saul, 1975). A smaller, shallow lake ($\pm 25 \times 75$ m) exists in the western part of the study area. Infrequently it is reduced to a small, muddy pool.

There are numerous swamps in depressions, and after heavy rains these and other low-lying areas offer extensive aquatic habitats that are drained by the numerous small streams.

CLIMATE

The climate at Santa Cecilia is typically *Af* in the Köppen classification, the climate type characteristic of the upper Amazon Basin (Eidt, 1969). Here we have essentially an aseasonal climate. This is not to say that fluctuations do not occur, but there are no distinct seasons. The only complete year of climatic data is for the period 29 June 1971 through

14 July 1972 (Fig. 8; Table 2). The following discussion also includes data from June-July, 1967, June-August, 1968, April-May, 1969, and April-May, 1973.

Winds are uncommon at Santa Cecilia; as often as not, a heavy rain may be preceded by a gentle breeze. Day length is nearly constant, and effective daylight is controlled more by cloud cover than by the seasonal position of the sun.

The daily temperature fluctuation is usually about 10° C. The greatest daily fluctuation recorded was 22-37° C on 9 August 1968; this also was the highest temperature recorded. The least fluctuation was 21.5-23.0 C on 22 April and 18 June 1972. The lowest temperature (17.0° C) was on the night of 17 June 1968. The lowest daily maximum temperatures and the lowest daily fluctuations are during periods of several days of continuous heavy cloud cover. Conversely, the highest daily maximum tem-



FIG. 7.—The west shore of the lower lake at Santa Cecilia.

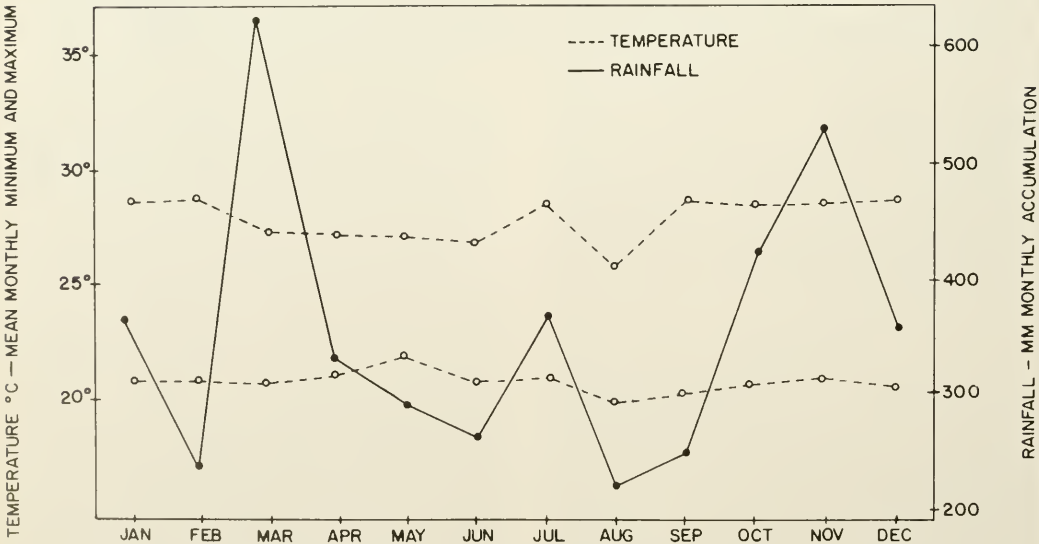


FIG. 8.—Monthly mean minimum and maximum ambient air temperatures and monthly rainfall accumulation at Santa Cecilia for the period July 1971-June 1972.

TABLE 2.—Summary of Climatic Data from Santa Cecilia.
(July 1971-June 1972)

Month	Rainfall (mm)			Cloud Cover (Days)		Temperature (° C)	
	Amount	Mean/Day	Days	Heavy	Clear	Maximum	Minimum
Jan	372.5	12.0	22	8	7	24.5-30.0	19.0-23.0
Feb	243.0	8.4	17	10	4	24.0-31.5	18.5-23.0
Mar	619.0	20.0	25	12	9	23.0-35.0	19.0-23.0
Apr	340.0	11.3	21	21	3	23.0-32.0	18.0-23.0
May	306.5	10.0	25	14	3	23.0-31.0	20.0-23.0
Jun	250.5	8.4	21	9	7	23.0-31.0	18.5-23.0
Jul	367.0	11.8	23	7	3	24.0-32.5	20.0-23.0
Aug	220.5	7.1	20	24	4	22.0-31.0	18.0-22.0
Sep	251.5	8.4	21	19	4	23.0-33.0	18.5-22.0
Oct	422.0	13.6	25	13	4	23.5-32.0	18.0-22.0
Nov	530.5	17.7	21	16	6	23.0-32.0	20.0-23.0
Dec	366.5	11.8	17	3	15	24.0-32.5	19.0-22.0
TOTAL	4289.5		215	156	69	22.0-35.0	18.0-23.0

peratures and the greatest daily fluctuations are during periods of clear weather.

Rainfall is abundant, but erratic; 4390 mm of rain were recorded in one year (Table 2). Local residents claim that normally August-September and December-February are drier than other times and that April-May and October-November have the heaviest rains. These observations are at least partially substantiated by data from 1971-1972, although in 1972, March with 619 mm of rain was the wettest month. In the period 3-23 March 1972 there were 393 mm of rain; in the same period in 1967 there were only 150 mm. Although in April-May 1972 there were only 646.5 mm of rain, the contention of the local residents was borne out in 1973, when 1335.5 mm fell in 30 days (Table 3). December 1971 was a relatively dry month with only 234 mm of rain in the first 29 days, but 114 mm fell on December 30. The only other records of rainfall in excess of 100 mm in a 24 hr period were in 1973: 26 April (390 mm), 1 May (105 mm), and 8 May (165 mm). Among the rainfall records for 20 months at Santa Cecilia, there are six instances of rainfall on more than ten consecutive days: 15-27 June 1967, 130 mm (1-34/day); 10-20 July 1968, 171 mm (2-46/day); 6-19 October 1971, 209 mm (1-54/day); 29 December 1971-9 January 1972, 281 mm (1-114/day); 8-21 May 1972, 166 mm (1-54/

day); 29 April-9 May 1973, 614 mm (2-165/day).

The number of consecutive days without rain varied from one in May to five in December, although there were more days that were predominately clear. The greatest number of consecutive clear days was nine in December. The rainfall pattern usually consists of three or four rainy days with a maximum of 50-70 mm for the period and a maximum of 30-50 mm on any given day, followed by one or two days without rain. The general pattern does fluctuate, however, and sometimes there are 8-10 consecutive days of moderate to heavy cloud cover with only 1-5 mm of rain each day. Conversely, it is possible to have several consecutive days of heavy rainfall, such as 29 April-5 May 1973, in which the daily rainfall was 70, 19, 105, 29, 90, 42,

TABLE 3.—Comparative Rainfall Data (mm) for Three Years.

10 June-9 July			
Year	1967	1968	1972
Total	322.0	304.0	330.5
No. Days	23	22	21
Daily Mean	10.7	10.1	11.0
Daily Range	0-71.0	0-50.0	0-22.5
19 April-18 May			
Year	1969	1972	1973
Total	378.0	316.0	1335.5
No. Days	20	24	22
Daily Mean	12.6	10.5	46.6
Daily Range	0-45.0	0-53.5	0-390.0



FIG. 9.—Aerial view of Santa Cecilia looking northeast. The Río Aguarico is visible in the lower right corner.

and 17 mm. This was followed by 2, 71, 165, and 4 mm, 3 days with no rain, and then 86, 38, and 46 mm. Generally, rain falls more frequently by day than at night. Rain was recorded on 215 days in the period July 1971-June 1972; of these, rain fell during the day and night on 47 days and only at night on 40 occasions. Sometimes rainfall is extremely localized during brief but heavy showers, whereas at times of extensive heavy cloud cover the entire region receives rain.

VEGETATION

Although plant collections have been made for the Shaw Herbarium of the Missouri Botanical Garden in St. Louis and the herbarium at the Universidad Católica in Quito, no published summary of the flora is available. Because the physiognomy determines the numbers and kinds of habitats available for animals, the following commentary is con-

cerned more with the structure of the vegetation than with the floristics.

Santa Cecilia is near the western limits of the largest expanse of tropical rain-forest in the world. This biotope called the *Hylea* by most South American biologists is referred to locally as the *selva*. The region of Santa Cecilia is at a sufficiently high elevation to preclude the seasonal flooding of great expanses of forest. Thus, the *bajiales* of the lower elevations of the Amazon Basin, characteristic as far inland as Iquitos, Perú, are absent.

Prior to 1965 we can assume that, with the exception of a few clearings along the river and scattered swamps, the entire region was covered with primary rain-forest (Fig. 9-10). This forest is best developed on level, well-drained ground. In such places the largest trees form a canopy 30-35 meters above the ground. Some stilt palms protrude through the canopy. The largest trees in the primary



FIG. 10.—Aerial view of Muñozlandia. The Río Aguarico is to the left. The large square building in the upper center is the laboratory.

forest are scattered 30-50 meters apart. Most such trees have extensive buttresses, that may extend 3 meters up the trunks, which may be up to 2 meters in diameter (Figs. 11-12). In some areas definite stratification can be found. A secondary stratum, when present, is 15-20 meters above the ground. This usually consists of broad-leafed trees, with or without buttresses, and stilt palms. A third layer at 8-12 meters consists of smaller, broad-leafed trees and spiny palms. The ground cover consists of a great variety of broad-leafed herbs 10-25 cm high and small ferns. In the primary forest there is a deep (5-10 cm) and continuous mulch layer. At midday usually no more than 10 percent of the ground cover receives sunlight. Lianas are numerous, and heavy growths of epiphytes are present on the horizontal limbs of the large trees, although bromeliads are uncommon. The large, buttressed trees forming the canopy have

shallow, extensive root systems. Growth seems to be limited by the ability of the shallow soil to hold the towering trees. These forest giants frequently fall over, with the uprooting of the extensive root system creating broad shallow craters and the interwoven system of lianas tearing a large swath in the forest. Thus,



FIG. 11.—Buttressed base of large tree in primary forest.



FIG. 12.—A trail through primary forest. Note the abundance of lianas.



FIG. 13.—Secondary forest. The large-leaved trees are *Cecropia*.



FIG. 14.—A forest-edge situation showing dense shrubby growth; in the foreground is a marsh.

there are numerous natural clearings in the primary forest.

Clearings, either natural or man-made, soon are overgrown by bushes, saplings, and the successional *Cecropia*. These trees attain heights of 10-12 meters. The secondary forest is characterized by dense, bushy undergrowth, few lianas, epiphytes, and herbs, and little mulch (Fig. 13). At the edge of either primary or secondary forest, especially along the borders of man-made clearings, there is a dense growth of various successional plants, especially leafy vines, which form an impenetrable wall of vegetation (Fig. 14).

Stands of bamboo with individual stalks reaching heights of 15-18 meters are scattered through the forest, although bamboo is uncommon in climax primary forest (Fig. 15).

Within both primary and secondary forest there are depressions that contain water at least intermittently. These swamps vary from small, shallow depres-



FIG. 15.—Bamboo grove in secondary forest.



FIG. 16.—A forest swamp that contained water throughout most of the year.

sions that are flooded only after heavy rains to large semi-permanent swamps (Fig. 16). The swamps in primary forest characteristically have numerous spiny palms, whereas the swamps in secondary forest usually support dense growths of *Heliconia*, the immense leaves of which attain lengths of 2 meters, exclusive of stems (Fig. 17).

Man-made clearings are either cultivated or maintained as clearings by man or grazing animals. Some *maíz* and pineapple are grown, but *plátanos* and *yuca* are the most common crops. As a result of topographic irregularities, there are low-lying areas in clearings that contain water. The marshes in these open depressions contain sawgrass, small *Heliconia*, and various aroids (Fig. 18).

HABITATS

Throughout the accounts of the species and in the ecological analysis, the data

are organized by major types of habitat. These are defined as follows:

Primary Forest.—Mature forest characterized by nearly continuous canopy, stratification of vegetation, and deep mulch layer.

Secondary Forest.—Successional stages and partially lumbered primary forest. The cutting of the large trees results in a physiognomy resembling that of intermediate successional stages.

Forest Edge.—The ecotone, usually resulting from human disturbance, between forest and clearings.

Bamboo.—Any of the stands of bamboo in forest or cleared areas.

Clearing.—Uncultivated clearings, usually man-made and characteristically supporting a variety of grasses.

Cultivated Fields.—Any cleared areas bearing crops.

Swamp.—Forest depressions containing water either ephemerally or permanently.



FIG. 17.—Dense growth of *Heliconia* in a shallow swamp.



FIG. 18.—A forest-edge marsh with a thick growth of sawgrass.

Marsh.—Water-filled depressions in clearings.

Lake.—This category includes only the two permanent lakes in the area.

River.—Only the two major water-

ways (Río Aguarico and Río Conejo) are included in this category.

Stream.—All flowing water not included in the former category.

IDENTIFICATION OF THE SPECIES

One of the most difficult problems that faces biologists working with the large Amazonian biota is the identification of the species. The following keys are offered as an aid to the identification of the species of amphibians and reptiles from the upper Río Aguarico. They should be useful for the herpetofauna of the entire upper Amazon Basin in Ecuador, southern Colombia, and northern Perú. Identifications made by use of the keys should be checked against the descriptions given in the accounts of the species.

The keys have been designed for use in the field with living or freshly preserved specimens. Unless stated otherwise, colors pertain to living animals. All characters used in the keys are visible with no more magnification than that provided by a 10 $\times$ hand lens. The keys are satisfactory for specimens of all ages, except that some juvenile frogs will present difficulties.

All character states, except the most obvious ones, are illustrated. Internal structures, such as dentition and hemipenes, have been avoided. The most confusing scutellation character in snakes is the loreal, a scale on the side of the head between the nasal and the preocular (Fig. 41a). Some snakes lack either the loreal scale or the preocular scale. If the scale that is present is higher than long, it is the preocular (Fig. 41c), whereas, if it is longer than wide, it is the loreal (Fig. 43b).

Uno de los problemas más difíciles que han enfrentado los biólogos a trabajar con la abundante biota amazónica ha sido la identificación de las especies. Las siguientes claves se entregan como una ayuda para la identificación de las especies de anfibios y reptiles de la región del alto Río Aguarico. Ellas deberían ser igualmente útiles para la herpetofauna de toda la Hoya Amazónica tanto en Ecuador, el sur de Colombia, como en norte de Perú. Las identificaciones hechas a través de estas claves deberían ser confrontadas con las descripciones dadas en los registros de especies.

Estas claves han sido diseñadas para su uso en el campo, trabajando con especímenes vivos o recientemente preservados. Si no menciona otra cosa, los colores corresponden a animales vivos. Todos los caracteres usados en las claves son visibles con no más aumento que el dado por una lupa manual de 10X. Las claves son satisfactorias para especímenes de toda edad, excepto para algunos sapos juveniles que presentarán un poco más de dificultad.

Todos los caracteres señalados, excepto los más obvios, son ilustrados. Las estructuras internas, tales como dentición y hemipenes, han sido evitados. De los caracteres de escutelación el que más confunde en las culebras es la escama loreal, ubicada lateralmente en la cabeza entre las escamas nasal y la preocular (Fig. 41a). En algunas culebras la loreal o la preocular están ausentes; en tal caso, si la escama presente es más alto que larga, es la preocular (Fig. 41c); si fuese más larga que ancha, corresponde a la loreal (Fig. 43b).

KEY TO THE ORDERS AND SUBORDERS
OF AMPHIBIANS AND REPTILES

1. Skin lacking external scales; limbs, if present, lacking claws on digits ... 2
 Skin covered with scales; limbs, if present, having claws on digits ... 4
2. Limbs absent
 Order Gymnophiona (p. 79)
 Limbs present 3
3. Tail present; hind limbs and forelimbs equal in size
 Order Caudata (p. 80)
 Tail absent; hind limbs much longer than forelimbs
 Order Anura (p. 82)
4. Body encased in a bony shell
 Order Testudines (p. 192)
 Body not encased in a bony shell 5
5. Limbs present 6
 Limbs absent 7
6. Nostrils dorsal; hind feet webbed; anal opening longitudinal
 Order Crocodilia (p. 194)
 Nostrils lateral; hind feet not webbed; anal opening transverse
 Suborder Sauria (p. 195)
7. Eyelids present; body cylindrical with small rectangular scales around body; anal opening nearly terminal
 Suborder Amphisbaenia (p. 224)
 Eyelids absent; body usually not cylindrical; scales not rectangular and not equal in size around the body; tail present posterior to the anal opening
 Suborder Serpentes (p. 224)

CLAVE DE ORDENES Y SUBORDENES
DE ANFIBIOS Y REPTILES

1. Piel sin escamas externas; extremidades, cuando presentes, no poseen uñas en los dedos 2
 Piel cubiertas de escamas; extremidades, cuando presentes, tienen uñas en los dedos 4
2. Extremidades ausentes
 Orden Gymnophiona (p. 79)
 Extremidades presentes 3
3. Cola presente; extremidades posteriores y anteriores de igual tamaño
 Orden Caudata (p. 80)
 Cola ausente; extremidades posteriores más largas que las anteriores
 Orden Anura (p. 82)
4. Cuerpo encerrado en una concha ósea Orden Testudines (p. 192)
 Cuerpo no encerrado en una concha ósea 5
5. Extremidades presentes 6
 Extremidades ausentes 7
6. Nostrilos dorsales; pies posteriores con membranas; ano con abertura longitudinal
 Orden Crocodilia (p. 194)
 Nostrilos laterales; pies posteriores sin membranas; ano con abertura transversal
 Suborden Sauria (p. 195)
7. Párpados presentes; cuerpo cilíndrico con pequeñas escamas rectangulares alrededor del cuerpo; ano con abertura casi terminal
 Suborden Amphisbaenia (p. 224)
 Párpados ausentes; cuerpo usualmente no cilíndrico; escamas no rectangulares e iguales en tamaño alrededor del cuerpo; cola presente posterior a la abertura anal
 Suborden Serpentes (p. 224)

KEY TO THE CAECILIANS

1. Small species, less than 200 mm in length; head pink or white, distinctly different from dark gray body *Microcaecilia albiceps* (p. 79)
Larger species; head same color as body 2
2. Body slender, length more than 80 times diameter 3
Body thick, length less than 50 times diameter 4
3. Eye visible beneath thin layer of bone¹ *Oscacecilia bassleri* (p. 80)
Eye in bony socket, not covered by bone *Caecilia disossea* (p. 79)
4. Snout tapered; body uniform dull bluish gray *Caecilia tentaculata* (p. 79)
Snout bluntly rounded; body bluish black with narrow white rings *Siphonops annulatus* (p. 80)

KEY TO THE SALAMANDERS

1. Belly dark with large, irregular pale blotches; snout-vent length to 60 mm *Bolitoglossa equatoriana* (p. 80)
Belly dull gray to brown, uniform or with minute pale flecks; snout-vent length to 40 mm *Bolitoglossa peruviana* (p. 80)

KEY TO THE FROGS

1. Fingers lacking expanded discs (Fig. 19c) 2

CLAVE DE LOS CECILIOS

1. Especie pequeña, menores de 200 mm de largo; cabeza rosada o blanca, notoriamente diferente del cuerpo gris oscuro *Microcaecilia albiceps* (p. 79)
Especie mayor; cabeza no diferente en color al cuerpo 2
2. Cuerpo delgado, largo mayor que 80 veces su diámetro 3
Cuerpo grueso, largo menor que 50 veces su diámetro 4
3. Ojo visible bajo una delgada capa ósea¹ *Oscacecilia bassleri* (p. 80)
Ojo en zoquete óseo, no cubierto por hueso *Caecilia disossea* (p. 79)
4. Hocico puntiagudo; cuerpo de color gris-azulado apagado uniformemente *Caecilia tentaculata* (p. 79)
Hocico romo, redondeado; cuerpo negro-azulado con anillos delgados blancos *Siphonops annulatus* (p. 80)

CLAVE DE LAS SALAMANDRAS

1. Vientre oscuro con manchas pálidas grandes e irregulares; distancia hocico-ano de 60 mm *Bolitoglossa equatoriana* (p. 80)
Vientre gris apagado a marrón, uniforme o con pequeñas pecas pálidas; distancia hocico-ano de 40 mm *Bolitoglossa peruviana* (p. 80)

CLAVE DE LOS SAPOS

1. Dedos sin discos terminales expandidos (Fig. 19c) 2

¹ In order to determine the nature of the eye, it is necessary to remove a flap of skin over the eye, which may be visible as a dark spot beneath the skin.

¹ Para determinar la naturaleza del ojo es necesario remover un pedacito de piel sobre el; el ojo puede verse como una mancha debajo de la piel.

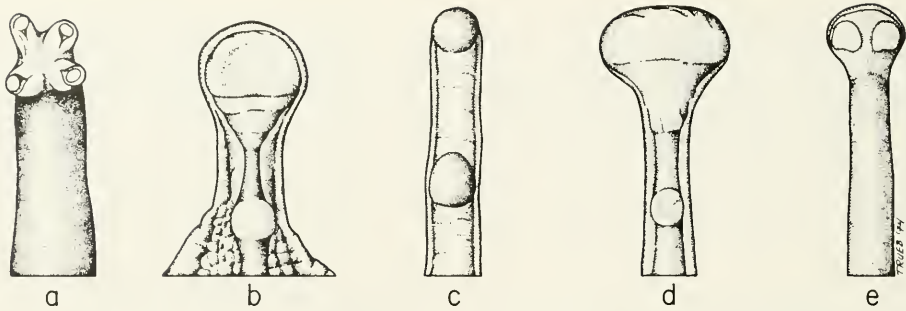


FIG. 19.—Digits of fingers: A. *Pipa pipa*, B. *Hyla geographica*, C. *Leptodactylus wagneri*, D. *Eleutherodactylus diadematus*, E. *Dendrobates pictus*; A-D ventral, E dorsal.

Fingers with expanded discs or other terminal modifications (Fig. 19a-b, d-e)		26	Dedos con discos expandidos u otra modificación terminal (Fig. 19a-b, d-e)		26
2.	Skin on belly smooth	3	2.	Piel del vientre suave	3
	Skin on belly granular	21		Piel del vientre granulosa	21
3.	Tympanum visible (Fig. 20b)	4	3.	Tímpano visible (Fig. 20b)	4
	Tympanum concealed (Fig. 20a)	17		Tímpano oculto (Fig. 20a)	17
a b					
FIG. 20.—Lateral views of heads: A. <i>Eleutherodactylus acuminatus</i> with tympanum concealed, B. <i>Eleutherodactylus lacrimosus</i> with tympanum (stippled) visible.					
4.	First finger shorter than second	5	4.	Primer dedo anterior más corto que el segundo	5
	First finger longer than or equal to second	7		Primer dedo anterior más largo que el segundo	7
5.	Four toes on foot (Fig. 21a)		5.	Cuatro dedos en los pies (Fig. 21a)	
	<i>Syncope antenori</i> (p. 192)			<i>Syncope antenori</i> (p. 192)	
	Five toes on foot (Fig. 21b)	6		Cinco dedos en los pies (Fig. 21b)	6

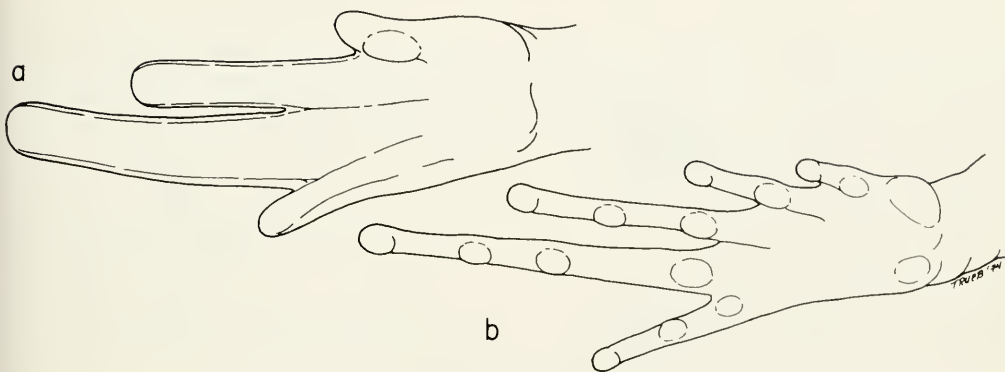


FIG. 21.—Ventral views of feet: A. *Syncope anteriori* with four toes, B. *Hamptophryne boliviana* with five toes.

- | | |
|---|---|
| <p>6. Dark brown anal patch; no dark triangular mark in occipital region; skin on dorsum smooth; snout broadly rounded
 <i>Eleutherodactylus nigrovittatus</i>
 (p. 96)</p> <p>No dark brown anal patch; dark triangular mark present in occipital region; skin on dorsum pustular; snout pointed
 <i>Adenomera andreae</i> (p. 83)</p> | <p>6. Mancha anal marrón oscura; sin marcas triangulares oscuras en la región occipital; piel del dorso suave; hocico ampliamente redondeado
 <i>Eleutherodactylus nigrovittatus</i>
 (p. 96)</p> <p>Sin mancha anal marrón oscura; marcas triangulares presentes en la región occipital; piel del dorso pustulosa; hocico puntiagudo
 <i>Adenomera andreae</i> (p. 83)</p> |
| <p>7. Outer toes webbed nearly to tips
 <i>Rana palmipes</i> (p. 186)</p> <p>Outer toes not or only basally webbed 8</p> | <p>7. Dedos posteriores externos con membranas hasta cerca de su extremo <i>Rana palmipes</i> (p. 186)</p> <p>Dedos posteriores externos sin o solamente con membranas en su base 8</p> |
| <p>8. Tubercles present on heels and eyelids <i>Edalorhina perezii</i> (p. 86)</p> <p>Tubercles absent on heels and eyelids 9</p> | <p>8. Tubérculos presentes en los talones y párpados
 <i>Edalorhina perezii</i> (p. 86)</p> <p>Tubérculos ausentes en los talones y párpados 9</p> |
| <p>9. Parotoid glands present (Fig. 22)
 <i>Bufo glaberrimus</i> (p. 116)</p> <p>Parotoid glands absent 10</p> | <p>9. Glándulas parótidas presentes (Fig. 22) <i>Bufo glaberrimus</i> (p. 116)</p> <p>Glándulas parótidas ausentes 10</p> |
| <p>10. Toes with distinct lateral fringes (Fig. 19c) 11</p> <p>Toes lacking lateral fringes 12</p> | <p>10. Dedos posteriores con flecos laterales (Fig. 19c) 11</p> <p>Dedos posteriores sin flecos laterales 12</p> |

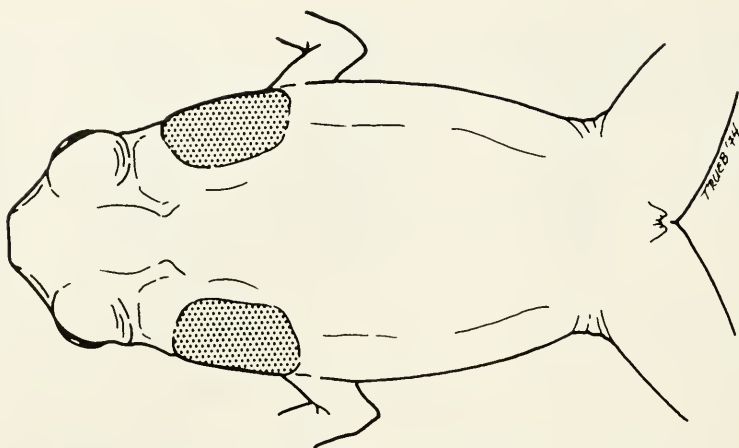


FIG. 22.—*Bufo glaberrimus* showing paratoid glands (stippled).

- | | |
|---|---|
| <p>11. First finger longer than second; venter mottled
 <i>Leptodactylus wagneri</i> (p. 112)
 First and second fingers equal in length; throat and chest dark; rest of venter usually creamy white
 <i>Leptodactylus discodactylus</i>
 (p. 105)</p> <p>12. Dorsum black with distinct cream or tan dorsolateral stripes; large red spots on thighs
 <i>Lithodytes lineatus</i> (p. 114)
 Not as described 13</p> <p>13. Dorsum tuberculate; orange spot with black mottling in groin; venter mottled pale gray and black with median white stripe
 <i>Physalaemus petersi</i> (p. 115)
 Dorsum smooth; coloration not as described 14</p> <p>14. Distinct cream or tan labial stripe 15
 Lips barred 16</p> | <p>11. Primer dedo anterior más largo que el segundo; vientre moteado
 <i>Leptodactylus wagneri</i> (p. 112)
 Primer y segundo dedos anteriores de igual longitud; garganta y pecho oscuros; el resto del vientre usualmente blanco cremoso
 <i>Leptodactylus discodactylus</i>
 (p. 105)</p> <p>12. Dorso negro, con bandas dorsolaterales distintas de color crema o marrón pálida; grandes manchas rojas en los muslos
 <i>Lithodytes lineatus</i> (p. 114)
 Diferente a lo descrito 13</p> <p>13. Dorso tuberculado; mancha anaranjada con pintas negras en la ingle; vientre moteado gris pálido con línea medial blanca
 <i>Physalaemus petersi</i> (p. 115)
 Dorso suave; coloración diferente a la descrita 14</p> <p>14. Franja labial resultante de color crema o marrón claro 15
 Labios con barras 16</p> |
|---|---|

15. Venter uniform cream
 Leptodactylus mystaceus (p. 107)
 Venter mottled cream and black
 Leptodactylus rhodomystax
 (p. 111)
16. Venter uniform grayish brown
 Leptodactylus stenodema (p. 112)
 Venter mottled cream and black
 Leptodactylus pentadactylus
 (p. 108)
17. Outer toe at least one-third webbed 18
 Outer toe not, or only basally,
 webbed 19
18. Dorsum and flanks dark; venter pale
 gray with dark spots
 *Chiasmocleis anatypes* (p. 187)
 Dorsum pale, sharply delineated
 from darker flanks; venter dark with
 pale flecks
 *Ctenophryne geayi* (p. 190)
19. Pale dorsal color meeting dark ven-
 tral color on a distinct line
 *Hamptophryne boliviana* (p. 190)
 Pale dorsal color blending into ven-
 tral color 20
20. Throat, chest, belly, and ventral sur-
 faces of thighs white with black
 spots and mottling
 *Chiasmocleis ventrimaculata*
 (p. 189)
 Throat and chest brown; belly and
 ventral surfaces of thighs white with
 black spots
 *Chiasmocleis bassleri* (p. 188)
21. Parotoid glands present (Fig. 22);
 outer toe more than one-third
 webbed 22
 Parotoid glands absent; outer toe
 not, or only basally webbed 23
15. Vientre uniformemente crema
 Leptodactylus mystaceus (p. 107)
 Vientre moteado de crema y negro ..
 Leptodactylus rhodomystax (p. 111)
16. Vientre uniformemente cafe-grisá-
 ceo
 *Leptodactylus stenodema* (p. 112)
 Vientre montada de crema y negro
 Leptodactylus pentadactylus
 (p. 108)
17. Dedo externo posterior al menos con
 membrana hasta un tercio de su lon-
 gitud 18
 Dedo externo posterior sin o sólo
 basalmente con membrana 19
18. Dorso y flancos oscuros; vientre gris
 pálido con manchas oscuras
 *Chiasmocleis anatypes* (p. 187)
 Dorso pálido, netamente delineado
 de los flancos oscuros; vientre oscuro
 con manchitas pálidas
 *Ctenophryne geayi* (p. 190)
19. Dorso de color pálido reuniéndose
 con colores ventrales oscuros en una
 línea distinta
 *Hamptophryne boliviana* (p. 190)
 Dorso de color pálido mezclándose
 con colores ventrales 20
20. Garganta, pecho, vientre, y caras
 ventrales de los muslos blancos
 con manchas y pintas negras
 *Chiasmocleis ventrimaculata*
 (p. 189)
 Garganta y pecho marrones; vientre
 y caras ventrales de los muslos blan-
 cos con manchas negras
 *Chiasmocleis bassleri* (p. 188)
21. Glándulas parótidas presentes (Fig.
 22); dedo externo posterior con más
 de un tercio con membrana 22
 Glándulas parótidas ausentes; dedo
 externo posterior sin o sólo basal-
 mente con membrana 23

22. First finger shorter than second; snout pointed; spinous lateral fold of skin *Bufo typhonius* (p. 118)
- First finger longer than second; snout rounded; no spinous lateral fold of skin *Bufo marinus* (p. 117)
23. First finger shorter than second 24
- First finger longer than second 25
24. Tympanum concealed (Fig. 20a); snout pointed; skin on dorsum spinous; venter reddish lavender *Dendrophryniscus minutus* (p. 120)
- Tympanum visible (Fig. 20b); snout rounded; skin on dorsum with elongate ridges; venter grayish cream *Eleutherodactylus sulcatus* (p. 102)
25. Dermal "horn" on upper eyelid; head broad ($> 50\%$ snout-vent length) *Ceratophrys cornuta* (p. 85)
- No dermal "horn" on upper eyelid; head narrow ($< 40\%$ snout-vent length) *Ischnocnema quixensis* (p. 104)
26. Fingers terminating in star-shaped structures (Fig. 19a); body greatly depressed *Pipa pipa* (p. 82)
- Fingers terminating in round or truncate discs (Fig. 19b, d, e); body not greatly depressed 27
27. Discs truncate; pair of dermal scutes on dorsal surface of each disc (Fig. 19e) 28
- Discs truncate or round; no dermal scutes on dorsal surface of each disc (Fig. 19b, d) 33
22. Primer dedo anterior más corto que el segundo; hocico puntiagudo; pliegue lateral de piel espinoso *Bufo typhonius* (p. 118)
- Primer dedo anterior más largo que el segundo; hocico redondeado; sin pliegue lateral de piel espinoso *Bufo marinus* (p. 117)
23. Primer dedo anterior más corto que el segundo 24
- Primer dedo anterior más largo que el segundo 25
24. Tímpano oculto (Fig. 20a); hocico puntiagudo; piel del dorso espinosa; vientre lavanda-rojizo *Dendrophryniscus minutus* (p. 120)
- Tímpano visible (Fig. 20b); hocico redondeado; piel del dorso con lomos alargados; vientre crema-grisáceo *Eleutherodactylus sulcatus* (p. 102)
25. "Cuerno" dérmico en el párpado superior; cabeza ancha ($> 50\%$ de la longitud hocico-ano) *Ceratophrys cornuta* (p. 85)
- Sin "cuerno" dérmico en el párpado superior; cabeza más estrecha ($< 40\%$ de la longitud hocico-ano) *Ischnocnema quixensis* (p. 104)
26. Dedos terminados en estructuras con forma de estrellas (Fig. 19a); cuerpo fuertemente deprimido *Pipa pipa* (p. 82)
- Dedos terminados en discos redondos o truncados (Fig. 19b, d, e); cuerpo no fuertemente deprimido 27
27. Discos truncados; un par de escudos dermales en la cara dorsal de cada disco (Fig. 19e) 28
- Discos truncados o redondeados; sin escudos dermales en la cara dorsal de cada disco (Fig. 19e) 33

28. First finger shorter than second
 *Colostethus sauli* (p. 123)
 First finger equal to or longer than
 second 29
29. Venter uniform white or pale yellow
 *Colostethus marchesianus* (p. 121)
 Venter mottled black and blue or
 gray 30
30. Dorsum brown with or without
 black flecks 31
 Dorsum red, or black with yellow
 lines 32
31. Pale ventrolateral stripe present;
 bright yellow spot on dorsal surface
 of upper arm and another in groin
 *Phyllobates femoralis* (p. 126)
 Pale ventrolateral stripe absent;
 bright yellow spot in groin and
 another on ventral surface of shank
 *Dendrobates pictus pictus*
 (p. 125)
32. Dorsum red
 *Dendrobates parvulus* (p. 124)
 Dorsum black with yellow lines
 *Dendrobates quinquevittatus*
 (p. 125)
33. Skin on belly smooth 34
 Skin on belly granular 35
34. Throat dark gray with median white
 stripe; no broad black mark posterior
 to eye
 *Eleutherodactylus lathanites*
 (p. 93)
 Throat and belly uniform creamy
 white; broad black mark present
 posterior to eye
 *Eleutherodactylus conspicillatus*
 (p. 89)
28. Primer dedo anterior más corto que
 el segundo
 *Colostethus sauli* (p. 123)
 Primer dedo anterior más largo que
 el segundo 29
29. Vientre uniformemente blanco o
 amarillo pálido
 *Colostethus marchesianus* (p. 121)
 Vientre montado negro y azul o
 gris 30
30. Dorso marrón con o sin pintas ne-
 gras 31
 Dorso rojo, o negro con líneas ama-
 rillas 32
31. Banda ventrolateral pálida presente;
 mancha amarilla brillante en la cara
 dorsal del brazo superior y otra en
 la ingle
 *Phyllobates femoralis* (p. 126)
 Banda ventrolateral pálida ausente;
 mancha amarilla brillante en la ingle
 y otra en la cara ventral de la canilla
 *Dendrobates pictus pictus* (p. 125)
32. Dorso rojo
 *Dendrobates parvulus* (p. 124)
 Dorso negro con líneas amarillas ..
 *Dendrobates quinquevittatus*
 (p. 125)
33. Piel del vientre suave 34
 Piel del vientre granulosa 35
34. Garganta gris oscura con banda
 blanca; sin ancha marca negra pos-
 terior al ojo
 *Eleutherodactylus lathanites*
 (p. 93)
 Garganta y vientre uniformemente
 blanco-cremoso; amplia marca ne-
 gra posterior al ojo presente
 *Eleutherodactylus conspicillatus*
 (p. 89)

35. First finger longer than second 36
First finger shorter than second 39
36. Head triangular with fleshy proboscis *Hemiphractus proboscideus* (p. 127)
Head normal without fleshy proboscis 37
37. Snout long, sloping; dermal fringes on outer edges of forearm and foot; white warts on dorsum
Centrolenella resplendens (p. 185)
Snout short, rounded; no dermal fringes on limbs; pale flecks, if present, not elevated 38
38. Dorsum dark green with small golden flecks; heart not visible through ventral skin; bones green
Centrolenella midas (p. 183)
Dorsum pale green with diffuse greenish yellow spots; heart visible through ventral skin; bones white
Centrolenella munozorum (p. 184)
39. First toe longer than second 40
First toe shorter than second 43
40. Flanks tan or orange with dark markings 41
Flanks green with or without cream, blue, or orange spots 42
41. Calcares absent (Fig. 23a); ventral side of head, flanks and venter cream or tan with brown or black flecks
Phyllomedusa palliata (p. 176)
35. Primer dedo anterior más largo que el segundo 36
Primer dedo anterior más corto que el segundo 39
36. Cabeza triangular con proboscis carnosa
Hemiphractus proboscideus (p. 127)
Cabeza normal sin proboscis carnosa 37
37. Hocico largo, en declive; flecos dérmicos en el canto externo del antebrazo y pie; verrugas blancas en el dorso
Centrolenella resplendens (p. 185)
Hocico corto, redondeado; sin flecos dérmicos en las piernas; pintas pálidas cuando presentes, no elevadas 38
38. Dorso verde oscuro con pequeñas manchas de color oro; corazón no visible a través de la pared ventral; huesos verdes
Centrolenella midas (p. 183)
Dorso verde pálido con manchas difusas amarilla-verdosas; corazón visible a través de la pared ventral; huesos blancos
Centrolenella munozorum (p. 184)
39. Primer dedo posterior más largo que el segundo 40
Primer dedo posterior más corto que el segundo 43
40. Flancos marrón claros o anaranjados con manchas oscuras 41
Flancos verdes con o sin manchas cremas, azules, o anaranjadas 42
41. Calcares ausentes (Fig. 23a); cara ventral de la cabeza, flancos y vientre crema o marrón claro con pecas marrones o negras
Phyllomedusa palliata (p. 176)

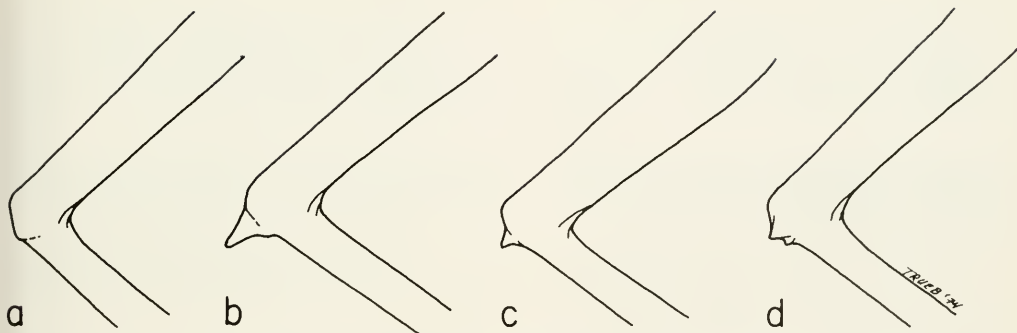


FIG. 23.—Dorsal views of heels showing presence and shape of calcars and tubercles: A. *Hyla punctata*, B. *Hyla calcarata*, C. *Hyla garbei*, D. *Hyla fasciata*.

Calcars present (Fig. 23a); side of head green; flanks orange with vertical black bars

..... *Phyllomedusa tomopterna*
..... (p. 179)

42. Parotoid region round; no dorsolateral row of white tubercles; iris deep bronze with black reticulations
..... *Phyllomedusa tarsius* (p. 177)

Parotoid region angular with dorsolateral row of white tubercles; iris pale green
..... *Phyllomedusa vaillanti* (p. 180)

43. Tympanum completely concealed (Fig. 20a) 44
At least ventral part of tympanum visible 46

44. Dorsum green with black stripe from snout to eye
..... *Eleutherodactylus acuminatus*
..... (p. 86)
Not as described 45

45. Small tubercle on heel (Fig. 23d); dorsum smooth
..... *Eleutherodactylus quaquaversus*
..... (p. 100)
No tubercle on heel; dorsum rugose
..... *Eleutherodactylus martiae* (p. 94)

Calcares presentes (Fig. 23b); lados de la cabeza verdes; flancos anaranjados con barras verticales negras
..... *Phyllomedusa tomopterna* (p. 179)

42. Región parótida redondeada sin fila dorsolateral de tubérculos blancos; iris bronce-oscuro con reticulaciones negras
..... *Phyllomedusa tarsius* (p. 177)

Región parótida angulosa con fila dorsolateral de tubérculos blancos; iris gris pálido
..... *Phyllomedusa vaillanti* (p. 180)

43. Tímpano completamente oculto (Fig. 20a) 44
Tímpano visible al menos en su parte ventral 46

44. Dorso verde con banda negra desde el hocico al ojo
..... *Eleutherodactylus acuminatus*
..... (p. 86)
Diferente a lo descrito 45

45. Pequeño tubérculo sobre el talón (Fig. 23d); dorso suave
..... *Eleutherodactylus quaquaversus*
..... (p. 100)
Sin tubérculo sobre el talón; dorso rugoso
..... *Eleutherodactylus martiae* (p. 94)

46. Outer toe not, or only basally, webbed 47
Outer toe more than one-third webbed 55
47. One elongate tubercle on heel (Fig. 23c); and two tubercles on margin of upper eyelid
Eleutherodactylus orphnolaimus (p. 98)
No tubercles on heel and eyelid 48
48. Bright yellow or orange spot in groin 49
No yellow or orange spot in groin 50
49. Spot in groin deep yellow or orange; spots widely separated ventrally; dorsum rugose.
Eleutherodactylus croceoinguinis (p. 90)
Spot in groin yellow, narrowly bordered by black; spots confluent, or nearly so, ventrally; dorsum smooth
Eleutherodactylus variabilis (p. 103)
50. Dorsum pale green, with or without cream dorsolateral stripe; discs on fingers round
Eleutherodactylus pseudoacuminatus (p. 99)
Dorsum not pale green; discs on fingers truncate 51
51. Venter pale green with white flecks
Eleutherodactylus paululus (p. 98)
Not as described 52
52. Upper lips with dark vertical or diagonal bars; venter not pale yellow 53
46. Dedo externo posterior sin o con membrana sólo en parte basal 47
Dedo externo posterior con membrana por más que un tercio 55
47. Un tubérculo alargado sobre el talón (Fig. 23c); y dos tubérculos sobre el márgen del párpado superior
Eleutherodactylus orphnolaimus (p. 98)
Sin tubérculos sobre el talón y el párpado 48
48. Mancha amarilla brillante o anaranjada en la ingle 49
Sin mancha amarilla o anaranjada en la ingle 50
49. Mancha inguinal amarilla oscura o anaranjada; manchas ampliamente separadas ventralmente; dorso rugoso
Eleutherodactylus croceoinguinis (p. 90)
Mancha inguinal amarilla, bordeada de negro; manchas juntándose o muy cercanas ventralmente; dorso suave
Eleutherodactylus variabilis (p. 103)
50. Dorso verde pálido, con o sin banda dorsolateral crema; discos de los dedos anteriores redondeados
Eleutherodactylus pseudoacuminatus (p. 99)
Dorso no verde pálido; discos de los dedos anteriores truncados 51
51. Vientre verde pálido con pecas blancas
Eleutherodactylus paululus (p. 98)
Diferente a lo descrito 52
52. Labios superiores con barras verticales o diagonales oscuras; vientre no amarillo pálido 53

- Upper lips not barred; venter immaculate pale yellow
Eleutherodactylus lacrimosus
 (p. 92)
53. Groin marked with bold vertical or diagonal dark marks separated by gray, blue, orange, or red areas 54
 Groin uniform brown
Eleutherodactylus ockendeni
 (p. 97)
54. Venter cream with brown reticulations
Eleutherodactylus diadematus
 (p. 91)
 Venter brown or gray with pale flecks
Eleutherodactylus altamazonicus
 (p. 87)
55. Outer finger not webbed 56
 Outer finger at least one-fourth webbed 64
56. Tubercle or calcar present on heel (Fig. 23b-d) 57
 No tubercles or calcars on heel (Fig. 23a) 59
57. Tubercle on heel (Fig. 23c); snout pointed, with tubercle on tip.
Hyla garbei (p. 144)
 Calcar on heel (Fig. 23b, d); snout rounded, without tubercle on tip
 58
58. Venter uniform white; flanks and thighs white or pale blue with vertical black bars
Hyla calcarata (p. 137)
 Venter white with small brown flecks; flanks and thighs white or pale blue with irregular black spots
Hyla fasciata (p. 140)
- Labios superiores sin barras; vientre amarillo pálido
Eleutherodactylus lacrimosus
 (p. 92)
53. Ingle marcada con notorias marcas verticales o diagonales separadas por áreas grises, azules, rojas, o anaranjadas 54
 Ingle uniformemente marrón
Eleutherodactylus ockendeni (p. 97)
54. Vientre crema con reticulaciones marrones
Eleutherodactylus diadematus
 (p. 91)
 Vientre marrón o gris con pecas pálidas
Eleutherodactylus altamazonicus
 (p. 87)
55. Dedo anterior externo sin membrana 56
 Dedo anterior externo al menos con membrana hasta un cuarto de su longitud 64
56. Tubérculo o calcar presente sobre el talón (Fig. 23b-d) 57
 Sin tubérculos o calcares sobre el talón (Fig. 23a) 59
57. Tubérculo sobre el talón (Fig. 23c); hocico puntiagudo, con proboscis sobre la punta
Hyla garbei (p. 144)
 Calcar sobre el talón (Fig. 23b, d); hocico redondeado, sin proboscis sobre la punta 58
58. Vientre blanco uniforme; flancos y muslos blancos o azul-pálidas con barras verticales negras
Hyla calcarata (p. 137)
 Vientre blanco con pequeñas pecas marrones; flancos y muslos blancos o azul-pálidas con manchas irregulares negras
Hyla fasciata (p. 140)

59. Skin co-ossified with roofing bones of skull; dorsum tan; other surfaces dark brown with large pale yellow spots on flanks and thighs *Nyctimantis rugiceps* (p. 168)
Not as described 60
60. Throat and chest grayish brown with cream spots on chest *Hyla lanciformis* (p. 150)
Throat and chest immaculate cream or yellow 61
61. Groin and anterior and posterior surfaces of thighs with black mottling enclosing yellow spots *Hyla rubra* (p. 163)
Groin and thighs not black with yellow spots 62
62. Dorsum pale brown with small black flecks; iris metallic green with black reticulations *Hyla alboguttata* (p. 128)
Not as described 63
63. Dorsum tan or pale olive-green with longitudinal brown marks; iris silver with median horizontal red streak. *Hyla cruentomma* (p. 139)
Dorsum pale green or yellowish tan with dark flecks, interorbital bar, and pairs of longitudinal or diagonal marks in scapular and sacral areas; iris bronze *Hyla funerea* (p. 143)
64. Calcar present on heel (Fig. 23b); pigmented reticulation present in lower eyelid (Fig. 24b) 65
No calcar on heel (Fig. 23a); no reticulation in lower eyelid (Fig. 24a) 66
59. Piel co-osificada con los heusos de la bóveda craneal; dorso marrón claro; otras superficies marrón oscuras con grandes manchas amarillo-pálidas sobre los flancos y muslos *Nyctimantis rugiceps* (p. 168)
Diferente a lo descrito 60
60. Garganta y pecho marrón-grisáceo con manchas cremas sobre el pecho *Hyla lanciformis* (p. 150)
Garganta y pecho de color crema o amarillo immaculados 61
61. Ingle y caras anteriores y posteriores de los muslos moteados de negro encerrando manchas amarillas *Hyla rubra* (p. 163)
Ingle y muslos no negros con manchas amarillas 62
62. Dorso marrón pálido con pequeñas pecas negras; iris verde metálico con reticulaciones negras *Hyla alboguttata* (p. 128)
Diferente a lo descrito 63
63. Dorso marrón claro o verde-oliva pálido con marcas longitudinales marrones; iris plateado con banda media horizontal roja *Hyla cruentomma* (p. 139)
Dorso verde pálido o marrón amarillento con pecas oscuras; barras interorbitales, y pares de marcas longitudinales od diagonales en la escápula y áreas sacrales; iris bronceado *Hyla funerea* (p. 143)
64. Calcar presente sobre el talón (Fig. 23b); párpado inferior con reticulación pigmentada (Fig. 24b) 65
Sin calcar sobre el talón (Fig. 23a); párpado inferior sin reticulación (Fig. 24a) 66

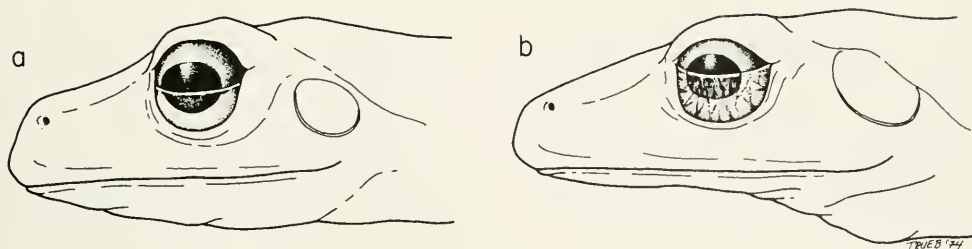


FIG. 24.—Lateral views of heads: A. *Hyla calcarata* with unpigmented lower eyelid, B. *Hyla geographica* with reticulated lower eyelid.

65. Outer finger webbed to base of disc; projecting prepollex in males (Fig. 25a) *Hyla boans* (p. 131)

Outer finger about three-fourths webbed; no projecting prepollex in males (Fig. 26b)
..... *Hyla geographica* (p. 146)

65. Dedo anterior externo con membrana hasta la base de los discos; prepolex saliente en los machos (Fig. 25a) *Hyla boans* (p. 131)

Dedo anterior externo con membrana hasta tres cuartos de su longitud; sin prepolex saliente en los machos (Fig. 25b)
..... *Hyla geographica* (p. 146)

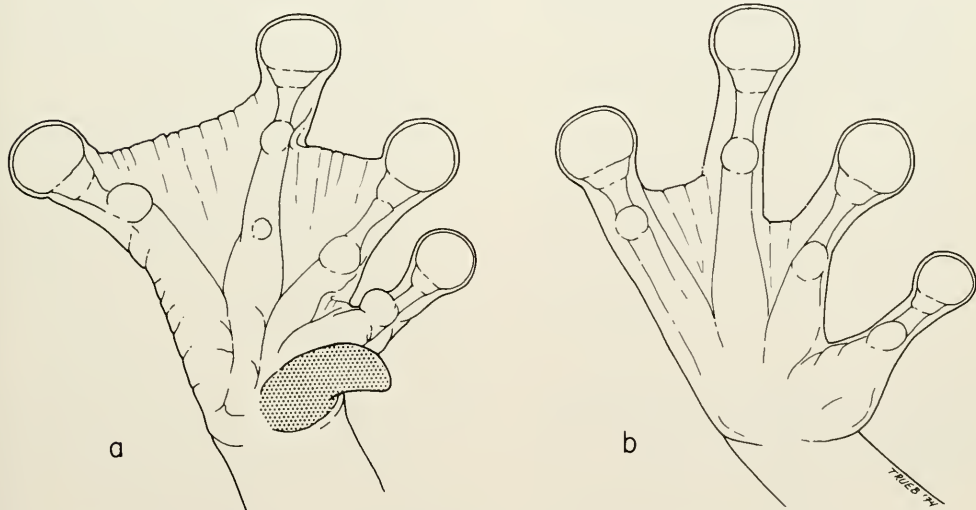


FIG. 25.—Palmar views of hands: A. *Hyla boans* with prepollex spine (stippled), B. *Hyla geographica* without prepollex spine.

66. Dorsum predominantly green, with or without red flecks or dorsolateral stripes 67
Not as described 70

66. Dorso predominantemente verde, con o sin pecas o bandas dorsolaterales rojas 67
Diferente a lo descrito 70

67. Snout pointed and angular in profile, projecting beyond margin of lip; vocal sac huge, pleated, pectoral (Fig. 26a) 68

Snout round, not projecting beyond margin of lip; vocal sac smooth, subgular (Fig. 26b) 69

67. Hocico puntiagudo y anguloso en perfil, proyectándose más allá del margen labial; inmenso saco vocal, rugoso, pectoral (Fig. 26a) 68

Hocico redondeado, no proyectándose más allá del margen labial; saco vocal suave, subgular (Fig. 26b) 69

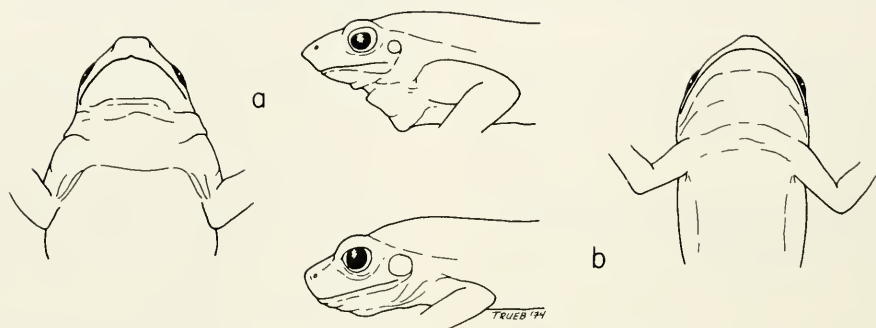


FIG. 26.—Ventral and lateral views: A. *Sphaenorhynchus eurhostus*, B. *Hyla punctata*.

68. Dorsum uniform green; outer finger webbed to base of disc; snout-vent length to 40 mm in males
..... *Sphaenorhynchus eurhostus*
..... (p. 182)

Dorsum green with narrow red dorsolateral lines; outer finger about one-half webbed; snout-vent length to 20 mm in males
..... *Sphaenorhynchus carneus*
..... (p. 181)

69. Dorsum uniform green or with transverse red marks; prepollical spine projecting in males
..... *Hyla granosa* (p. 148)

Dorsum green with red flecks and/or dorsolateral stripes; no projecting prepollical spine
..... *Hyla punctata* (p. 158)

70. Outer finger at least two-thirds webbed 71

68. Dorso verde uniforme; dedo anterior externo con membrana hasta la base del disco; longitud hocico-ano de hasta 40 mm en machos
..... *Sphaenorhynchus eurhostus*
..... (p. 182)

Dorso verde con líneas delgadas dorsolaterales rojas; dedo anterior externo con membrana hasta su mitad; longitud hocico-ano de hasta 20 mm en machos
..... *Sphaenorhynchus careus* (p. 181)

69. Dorso verde uniforme o con marcas rojas transversales; espina prepollical saliente en machos
..... *Hyla granosa* (p. 148)

Dorso verde con pecas y/o bandas dorsolaterales rojas; sin espina prepollical saliente
..... *Hyla punctata* (p. 158)

70. Dedo anterior externo con membrana hasta al menos dos tercios de su longitud 71

- Outer finger no more than one-half webbed 74
71. Belly orange or yellow with bold black mottling; webbing orange; dermal fringes present on outer edges of forearm and foot
..... *Hyla marmorata* (p. 153)
Not as described 72
72. Broad, vertical cream bar below eye, expanded into labial stripe in some females; skin on dorsum of males spinous, of females, smooth
..... *Osteocephalus taurinus* (p. 172)
No suborbital bar or labial stripe; skin on dorsum thick and glandular 73
73. Large black post-tympanic spot present; webbing red; large dark brown quadrangular dorsal blotch narrowly outlined with cream
..... *Phrynohyas coricea* (p. 173)
No black post-tympanic spot; webbing tan; dorsal pattern variable, but usually not consisting of a large quadrangular blotch
..... *Phrynohyas venulosa* (p. 174)
74. Dorsum tan or olive usually with narrow transverse dark markings; cream labial stripe usually expanded posteroventral to eye; dorsum in males bearing many small spinous tubercles
..... *Osteocephalus leprieurii* (p. 171)
Not as described 75
75. Dorsum mottled dark brown, green, and tan; lips at least faintly barred with dark brown or dark green; dorsum in males bearing mixture of large and small tubercles
..... *Osteocephalus buckleyi* (p. 170)
- Dedo anterior externo con membrana hasta no más allá de su mitad 74
71. Vientre anaranjado o amarillo con motas negras oscuras; membranas anaranjadas; cantos dérmicos presentes en los costados externos de los antebrazos y pies
..... *Hyla marmorata* (p. 153)
Diferente a lo descrito 72
72. Amplia barra vertical crema bajo eo ojo, expandiéndose hacia una banda labial en algunas hembras; piel de los machos espinosa, de las hembras suave
..... *Osteocephalus taurinus* (p. 172)
Sin barra suborbital o banda labial; piel del dorso gruesa y glandular 73
73. Gran mancha negra postimpánica presente; membranas rojas; gran mancha dorsal cuadrangular marrón limitada por fino borde crema
..... *Phrynohyas coriacea* (p. 173)
Sin mancha negra postimpánica; membranas marrones claras; colores dorsales variables, usualmente sin una gran mancha cuadrangular
..... *Phrynohyas venulosa* (p. 174)
74. Dorso marrón claro u oliva, corrientemente con marcas transversales oscuras; banda labial crema casi siempre expandida posteroventralmente al ojo; dorso de los machos con pequeños tubérculos espinosos
..... *Osteocephalus leprieurii* (p. 171)
Diferente a lo descrito 75
75. Dorso moteado marrón oscuro, verde, y marrón claro; labios al menos suavemente pintados con barras marrones oscuros o verdes oscuros; dorso de los machos con una mezcla de tubérculos grandes y pequeños
..... *Osteocephalus buckleyi* (p. 170)

Not as described	76	Diferente a lo descrito	76
76. Dorsum cream or yellow with red- dish brown flecks and broad lateral stripe <i>Hyla rhodopepla</i> (p. 159)		76. Dorso crema o amarillo con pecas y amplia banda lateral marrón-rojiza <i>Hyla rhodopepla</i> (p. 159)	
Not as described	77	Diferente a lo descrito	77
77. Thighs dark brown or black with one to three cream or yellow spots on dorsal surface	78	77. Muslos marrón-oscuros o negros, con una a tres manchas amarillas sobre la cara dorsal	78
Thighs not so patterned	80	Muslos con otro diseño	80
78. Venter gray and white with bright orange spot on proximal ventral sur- face of shank; one white suborbital bar <i>Hyla parviceps</i> (p. 156)		78. Vientre gris y blanco con mancha anaranjado brillante sobre la parte proximal de la cara ventral de la canilla; una barra suborbital blanca <i>Hyla parviceps</i> (p. 156)	
Venter creamy white; no orange spot on shank; two white suborbital bars	79	Vientre blanco-cremoso; sin mancha anaranjada en la canilla; dos barras suborbitales blancas	79
79. Anterior surface of thigh uniform dark brown		79. Cara anterior del muslo marrón-os- cura uniforme	
..... <i>Hyla brevifrons</i> (p. 135)		 <i>Hyla brevifrons</i> (p. 135)	
Anterior surface of thigh dark brown with one large yellow spot ...		Cara anterior del muslo marrón- oscura con una mancha grande ama- rilla <i>Hyla bokermanni</i> (p. 133)	
..... <i>Hyla bokermanni</i> (p. 133)			
80. Webbing and hidden surfaces of thighs orange or red	81	80. Membranas y caras escondidas de los muslos anaranjadas o rojas ...	81
Webbing and hidden surfaces of thighs brown or yellow	84	Membranas y caras escondidas de los muslos marrones o amarillas ..	84
81. Webbing and hidden surfaces of thighs red (pink at night)		81. Membranas y caras escondidas de los muslos rojas (rosadas por la noche) ... <i>Hyla triangulum</i> (p. 167)	
..... <i>Hyla triangulum</i> (p. 167)			
Webbing and hidden surfaces of thighs orange	82	Membranas y caras escondidas de los muslos anaranjadas	82
82. Dorsum dark brown with a network of cream lines		82. Dorso marrón oscuro con un enre- jado de líneas cremas	
..... <i>Hyla favosa</i> (p. 142)		 <i>Hyla favosa</i> (p. 142)	
Not as described	83	Diferente a lo descrito	83

83. Dorsolateral light bands straight-edged, continuing onto and usually fusing on rump, enclosing hour-glass-shaped dark brown dorsal mark; dorsal surfaces of shanks predominately pale with or without one narrow dark crossbar
 *Hyla leucophyllata* (p. 152)
- Dorsolateral light bands irregular, extending diagonally to point behind arms; dorsal surfaces of shanks brown with broad, irregular, pale crossbar
 *Hyla sarayacuensis* (p. 165)
84. Distinct light spots or transverse lines above anus and on heels 85
- No light spots or lines above anus and on heels 86
85. Dorsum dark brown with light top of snout, dorsolateral stripes, and round spots—one on rump and each heel *Hyla bifurca* (p. 130)
- Dorsum tan with brown blotches narrowly outlined with cream; cream line above anus and on each heel *Hyla minuta* (p. 155)
86. Three white spots on upper lip; dorsum tan with dark brown blotch or chevrons *Hyla riveroi* (p. 161)
- Upper lip unmarked; dorsum tan with dark brown flecks or irregular lines *Hyla rossalleni* (p. 162)
83. Bandas dorsolaterales tenues con bordes rectos, continuándose y eorrientemente fusionándose en la nalga, encerrando a una mancha marrón-oscuro en forma de reloj de arena; cara dorsal de la pierna predominantemente pálida con o sin una delgada barra cruzada oscura
 *Hyla leucophyllata* (p. 152)
- Bandas dorsolaterales no acentuadas irregulares, extendiéndose diagonalmente hasta detrás de los brazos; cara dorsal de la pierna marrón con una barra cruzada ancha, irregular, pálida
 *Hyla sarayacuensis* (p. 165)
84. Manchas claras resaltantes o líneas transversales por encima del ano y de los talones 85
- Sin manchas elaras o líneas por encima del ano y de los talones 86
85. Dorso marrón oscuro con la punta del hocico clara, bandas dorso-laterales, y manchas redondeadas—una sobre el anca y otra en cada talón
 *Hyla bifurca* (p. 130)
- Dorso marrón claro con manchas irregulares marrones delimitadas por crema; línea crema por encima del ano y sobre cada talón
 *Hyla minuta* (p. 155)
86. Tres pintas blancas sobre el labio superior; dorso marrón claro con mancha marrón o en bandas diagonales formando una V
 *Hyla riveroi* (p. 161)
- Labio superior sin marcas; dorso marrón con pecas marrones oscuras o con líneas irregulares
 *Hyla rossalleni* (p. 162)

KEY TO THE TURTLES

CLAVE DE LA TORTUGAS

1. Neck folds laterally to lie along margin of shell 2
 Neck withdraws straight back into shell 5
2. Head broad, flat, with fleshy proboscis and many long barbels; carapace broad, depressed, with ridges of keeled scutes
 Chelus fimbriatus (p. 192)
 Not as described 3
3. Two rounded, longitudinal ridges on carapace; lateral edges of carapace upturned
 Platemys platycephala (p. 193)
 Not as described 4
4. Margin of posterior plastral indentation concave (Fig. 27a); plastron dark; throat dusky
 Mesoclemmys gibba (p. 192)
 Margin of posterior plastral indentation convex (Fig. 27b); plastron pale with or without dark spots; throat cream with black spots
 Phrynops Geoffroanus tuberosus
 (p. 193)

1. Cuello plegado lateralmente fuera de la concha 2
 Cuello se retrae directamente dentro la concha 5
2. Cabeza ancha, chata, con proboscis carnosa y muchas barbillas; carapacho ancho, deprimido, con las salientes de los escutelos quillados
 Chelus fimbriatus (p. 192)
 Diferente a lo descrito 3
3. Dos crestas longitudinales redondeadas en el carapacho; márgenes laterales del carapacho dispuestos hacia arriba
 Platemys platycephala (p. 193)
 Diferente a lo descrito 4
4. Márgen de la indentación plastral posterior cóncava (Fig. 27a); plastrón oscuro; región gular terrosa
 Mesoclemmys gibba (p. 192)
 Márgen de la indentación plastral posterior convexa (Fig. 27b); plastrón pálido con o sin manchas oscuras; región gular crema con manchas negras
 Phrynops Geoffroanus tuberosus
 (p. 193)

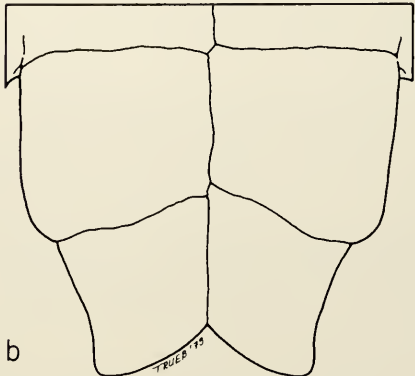
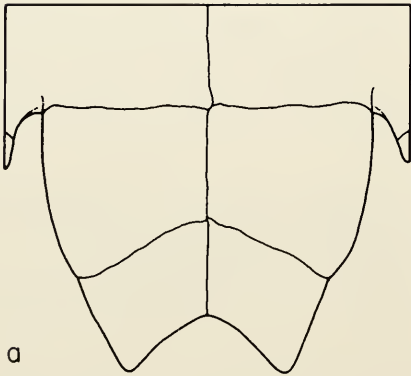


FIG. 27.—Posterior margins of plastra: A. *Mesoclemmys gibba*, B. *Phrynops Geoffroanus*.

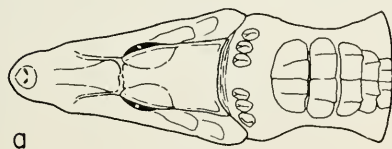
5. Carapace high, domed; feet short, stubby
Geochelonia denticulata (p. 194)

Carapace rounded, with three longitudinal ridges; feet broad, webbed
Kinosternon scorpioides (p. 194)

KEY TO THE CROCODYLIANS

1. A transverse bony ridge anterior to orbits; two or three transverse rows of occipital scales (Fig. 28a)
Caiman crocodilus crocodilus
 (p. 194)

No transverse bony ridge anterior to orbits; one transverse row of greatly enlarged, strongly keeled occipital scales (Fig. 28b)
Paleosuchus trigonatus (p. 195)



a

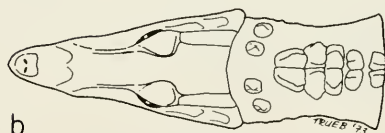
5. Carapacho alto, en forma de cúpula; pies cortos, gruesos
Geochelonia denticulata (p. 000)

Carapacho redondo, con tres crestas longitudinales; pies anchos palmeados
Kinosternon scorpioides (p. 194)

CLAVE DE LOS COCODRILOS

1. Una cresta ósea transversal anterior a las órbitas; dos o tres hileras transversales de escamas occipitales (Fig. 28a)
Caiman crocodilus crocodilus
 (p. 194)

Sin cresta ósea transversal anterior a las órbitas; una hilera transversal de escamas occipitales grandes fuertemente guilladas (Fig. 28b)
Paleosuchus trigonatus (p. 195)



b

FIG. 28.—Dorsal views of head and neck: A. *Caiman crocodilus*, B. *Paleosuchus trigonatus*.

KEY TO THE
LIZARDS AND AMPHISBAENIANS

1. Feet (at least forefeet) present; eye distinct 2
 Limbs absent; eye reduced to an indistinct spot covered with skin
Amphisbaena fuliginosa (p. 224)

2. Lower eyelid absent; dorsal scales small, granular, those on top of head same size as scales on middorsum of body 3

Lower eyelid present; scales on top of head not granular, differing from those on middorsum of body 5

CLAVE DE LOS LAGARTOS Y ANFISBAENAS

1. Pies (al menos los anteriores) presentes; ojo distinto 2

Sin extremidades; ojo reducido a una mancha indistinta cubierta de piel
Amphisbaena fuliginosa (p. 224)

2. Párpado inferior ausente; escamas dorsales pequeñas, granulares, aquellas en la superficie de la cabeza del mismo tamaño que aquellas en la mitad dorsal del cuerpo 3

Párpado inferior presente; escamas cefálicas no granulares difiriendo de aquellas en la mitad dorsal del cuerpo 5

3. Toes having greatly expanded adhesive pads in two rows (Fig. 29a)
... *Thecadactylus rapicauda* (p. 197)
Toes not having adhesive pads 4

4. Claws covered by scaly sheath (Fig. 29b); scales on belly pointed posteriorly; nuchal collar absent; body dark brown; top of head tan; throat white with brown streaks; tail not banded
... *Pseudogonatodes guianensis*
..... (p. 196)
Claws not covered by scaly sheath (Fig. 29c); scales on belly broadly rounded posteriorly; narrow white nuchal collar usually present; females brown with dark brown transverse marks or reticulations; males with orange head and black and white mottled body; tail usually banded tan and dark brown
..... *Gonatodes concinnatus* (p. 195)
3. Dedos con cojinetes adhesivos muy expandidos, dispuestos en dos hileras (Fig. 29a)
... *Thecadactylus rapicauda* (p. 197)
Dedos sin cojinete adhesivos 4

4. Garras cubiertas por una vaina escamosa (Fig. 29b); escamas ventrales orientadas hacia atrás; collar nuchal ausente; cuerpo marrón oscuro; parte superior de la cabeza bronceado; región gular blanca con rayas marrones; cola sin bandas
... *Pseudogonatodes guianensis*
..... (p. 196)
Garras no cubiertas por una vaina escamosa (Fig. 29c); escamas ventrales ampliamente redondeadas posteriormente; collar nuchal blanco, angosto, generalmente presente; hembras marrones con marcas o reticulaciones transversales marrón oscuras; machos con la cabeza anaranjada y cuerpo moteado de blanco y negro; cola generalmente con bandas bronceadas y marrón oscuras
..... *Gonatodes concinnatus* (p. 195)

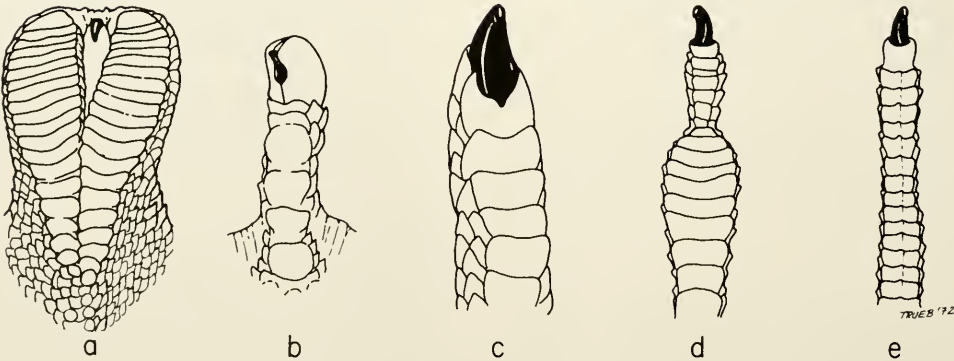


FIG. 29.—Ventral views of digits: A. *Thecadactylus rapicauda*, B. *Pseudogonatodes guianensis*, C. *Gonatodes concinnatus*, D. *Anolis fuscoauratus*, E. *Plica umbra*.

5. Top of head covered with granular or irregular flat scales, the largest usually arranged in semicircles between the eyes (Fig. 30a); lacking median frontal plate between eyes; tongue fleshy, not extensible 6

Top of head with regular flat plates; median frontal plate between eyes (Fig. 30c); tongue extensible, bifurcate 16

5. Superficie de la cabeza con escamas planas granulares o irregulares, las más grandes usualmente dispuestas en semicírculos entre los ojos (Fig. 30a); sin placa media frontal entre los ojos; lengua carnosa, no extensible 6

Superficie de la cabeza con placas chatas regulares; con placa frontal media entre los ojos (Fig. 30c); lengua bifurcada extensible 16

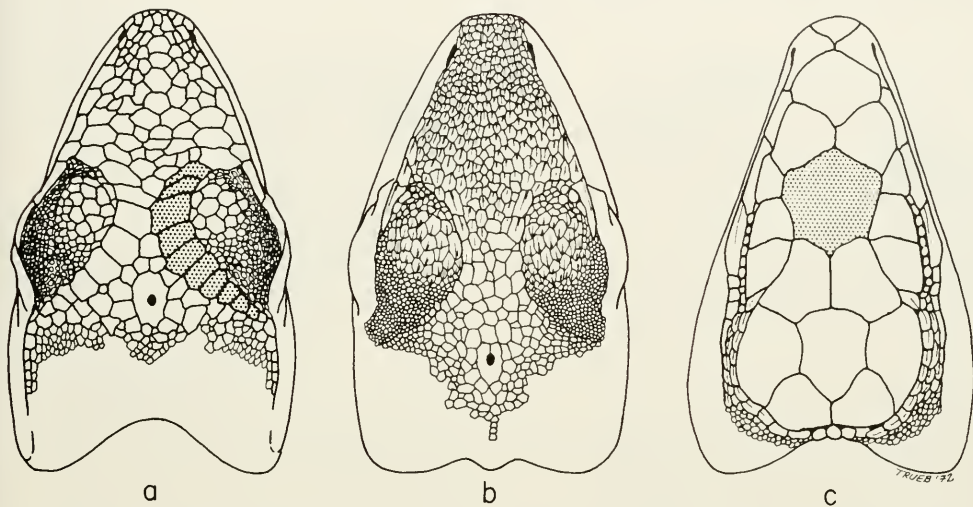


FIG. 30.—Dorsal views of heads: A. *Anolis transversalis* with smooth scales and enlarged supraorbital semicircular scales (stippled on right side), B. *Anolis trachyderma* with keeled scales and small supraorbital semicircular scales, C. *Kentropyx pelviceps* with regular cephalic plates, including a median frontal plate (stippled).

6. Tail having spiny scales arranged in transverse whorls (Fig. 31a, c) 7

Tail not having spiny scales arranged in transverse whorls (Fig. 31b) 9

7. Tail cylindrical, covered with rings of small scales; a middorsal crest of long, spiny scales (Fig. 32a) 8

Tail flattened in horizontal plane, short; all caudal scales large and spiny (Fig. 31c); body and tail black; head orange *Uracentron flaviceps* (p. 208)

6. Cola con escamas espinosas dispuestas en anillos transversales (Fig. 31a, c) 7

Cola sin escamas espinosas dispuestas en anillos transversales (Fig. 31b) 9

7. Cola cilíndrica, cubierta con anillos de escamas pequeñas; una cresta media dorsal de escamas espinosas grandes (Fig. 32a) 8

Cola achatada en plano horizontal, corta; todas las escamas caudales grandes y espinosas (Fig. 31c); cuerpo y cola negros; cabeza anaranjada *Uracentron flaviceps* (p. 208)

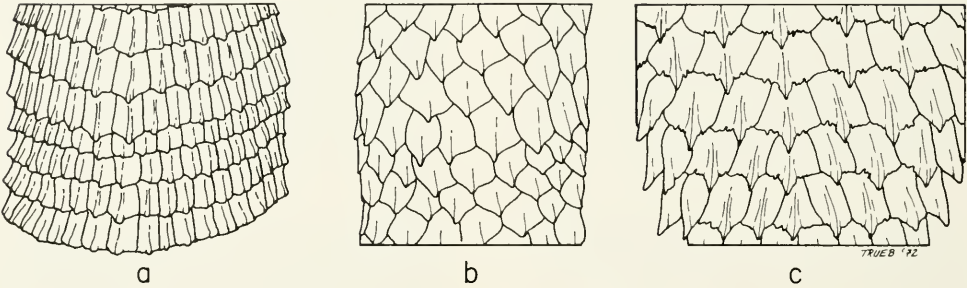


FIG. 31.—Dorsal views of proximal segments of tails: A. *Enyalioides laticeps*, B. *Plica umbra*, C. *Uracentron flaviceps*.

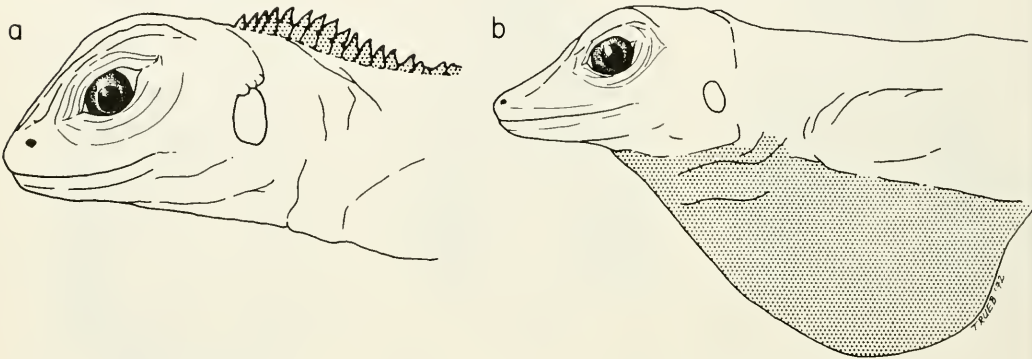


FIG. 32.—Lateral views of A. *Enyalioides laticeps* with middorsal crest (stippled), B. *Anolis transversalis* with dewlap (stippled).

8. A dorsolateral row of enlarged spiny scales on body
 Enyalioides cofanorum (p. 203)

No dorsolateral row of enlarged scales
 Enyalioides laticeps festae (p. 204)

9. Toes dilated and flattened (Fig. 29d); gular dewlap present at least in males (Fig. 32b) 10

Toes cylindrical or laterally compressed (Fig. 29c); gular dewlap absent 15
8. Con hilera dorsolateral de escamas espinosas dilatadas en el cuerpo
 Enyalioides cofanorum (p. 203)

Sin hilera dorsolateral de escamas espinosas dilatadas en el cuerpo
 Enyalioides laticeps festae (p. 204)

9. Dedos dilatados y aplanados (Fig. 29d); abanico gular presente, al menos en los machos (Fig. 32b) 10

Dedos cilíndricos o lateralmente comprimidos (Fig. 29c); abanico gular ausente 15

10. Supraorbital scales large, smooth (Fig. 30a); other dorsal head scales smooth, or only scales on snout keeled; ventral scales large, smooth or weakly keeled 11
Supraorbital scales small, strongly keeled (Fig. 30b), or median supraorbitals enlarged, keeled; all other dorsal head scales keeled; ventrals keeled, smooth, or granular 13
11. All head scales smooth: dorsum green or tan with bold diagonal transverse dark brown lines or bars; dewlap pale yellow with black bars *Anolis transversalis* (p. 202)
Scales on tip of snout keeled; coloration not as described 12
12. Ventral scales weakly keeled; dorsum green (blue-gray in preservative) with bluish white flecks; scales around eye yellow; dewlap orange-yellow with white scales
Anolis punctatus Boulengeri (p. 201)
Venter scales smooth; dorsum tan or gray, mottled with brown; venter creamy tan; dewlap orange with red streaks *Anolis ortonii* (p. 200)
13. Ventral scales large, keeled; dorsum brown with diagonal dark brown streaks and/or cream middorsal line; belly cream with brown streaks; dewlap red peripherally, blue with white scales medially
Anolis chrysolepis scypheus (p. 198)
Ventral scales smooth; coloration not as described 14
10. Escamas supraorbitales grandes, lisas (Fig. 30a); las otras escamas dorsales de la cabeza lisas o solamente quilladas en el hocico; escamas ventrales grandes, lisas o ligeramente quilladas 11
Escamas supraorbitales pequeñas, fuertemente quilladas (Fig. 30b), o las supraorbitales medianas dilatadas, quilladas; todas las otras escamas dorsales de la cabeza quilladas; ventrales quilladas, lisas o granulares 13
11. Todas las escamas de la cabeza lisas; dorso verdoso o bronceado con líneas o barras diagonales transversales marrón oscuras; abanico gular amarillo pálido con barras negras
Anolis transversalis (p. 202)
Escamas en la punta del hocico quilladas; coloración diferente a lo descrito 12
12. Escamas ventrales ligeramente quilladas; dorso verdoso (azul grisáceo en preservativo) con puntos blanco-azulados; escamas alrededor del ojo amarillas; abanico gular anaranjado amarillento con escamas blancas
Anolis punctatus Boulengeri (p. 201)
Escamas ventrales lisas; dorso bronceado o grisáceo, moteado de marrón; vientre cremoso bronceado; abanico gular anaranjado con rayas rojas *Anolis ortonii* (p. 200)
13. Escamas ventrales grandes quilladas; dorso marrón con rayas diagonales marrón oscuro y/o línea mediodorsal crema; vientre crema con rayas marrones; abanico gular rojo en la periferia, azul con escamas blancas en el centro
Anolis chrysolepis scypheus (p. 198)
Escamas ventrales lisas; coloración diferente a lo descrito 14

14. Ventral scales smaller, nearly granular; throat and belly white, heavily flecked with brown or gray; dewlap rose-pink with white scales and white margin
Anolis fuscoauratus fuscoauratus (p. 199)

Ventral scales larger, flat; belly dark gray laterally, yellow or creamy white medially; chin dark with transverse yellow line; dewlap orange-red with black scales
Anolis trachyderma (p. 201)

15. Middorsal crest present; tail less than twice length of body
Plica umbra ochrocollaris (p. 206)
- Middorsal crest absent; tail more than twice length of body
Polychrus marmoratus (p. 207)

16. Dorsal scales heterogeneous; large keeled scales mixed with small granular scales (Fig. 33a) 17
- Dorsal scales homogeneous or nearly so 18

14. Escamas ventrales más pequeñas, casi granulares; región gular y vientre blancos, profusamente moteado de marrón o gris; abanico gular rosado con el margen y las escamas blancas
Anolis fuscoauratus fuscoauratus (p. 199)

Escamas ventrales más grandes, planas; vientre lateralmente gris oscuro, amarillo o blanco cremoso en el centro; mentón oscuro con una línea transversal amarilla; abanico gular rojo-anaranjado con escamas negras
Anolis trachyderma (p. 201)

15. Cresta media dorsal presente; cola menos de dos veces la longitud del cuerpo
Plica umbra ochrocollaris (p. 206)
- Cresta media dorsal ausente; cola más de dos veces la longitud del cuerpo
Polychrus marmoratus (p. 207)

16. Escamas dorsales heterogéneas; escamas grandes quilladas mezcladas con las escamas granulares pequeñas (Fig. 33a) 17
- Escamas dorsales homogéneas o casi homogéneas 18

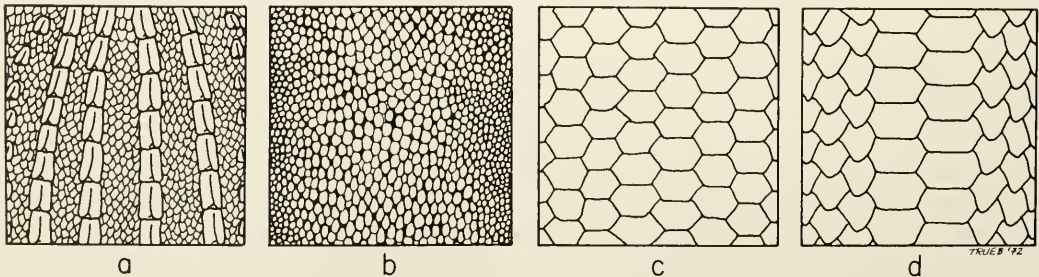


FIG. 33.—Dorsal views of body scutellation: A. *Neusticurus cephalopus*, B. *Kentropyx pelviceps*, C. *Mabuya mabouya*, D. *Iphisa elegans*.

17. Small (total length less than 200 mm); median ventral scales smooth; snout pointed; black spot with light center above insertion of arm *Neusticurus ecpleopus* (p. 218)
- Large (total length to 850 mm); median ventral scales slightly keeled; snout blunt; no black spot above insertion of arm *Dracaena guianensis* (p. 214)
18. Dorsal scales granular, much smaller than ventrals (Fig. 33b) 19
- Dorsal scales not granular, as large as, or only slightly smaller than ventrals 21
19. Ventral scales in more than 20 longitudinal rows; dorsal scales smooth *Tupinambis tequixin* (p. 223)
- Ventral scales in fewer than 17 longitudinal rows; dorsal granules small, rounded or keeled 20
20. Ventral scales keeled *Kentropyx pelviceps* (p. 215)
- Ventral scales smooth *Ameiva ameiva petersii* (p. 210)
21. Hind limbs normal 22
- Hind limbs reduced to small stubs *Bachia trinasale trinasale* (p. 213)
22. Dorsal scales smooth 23
- Dorsal scales keeled 24
23. All dorsal body scales about equal in size (Fig. 33c) *Mabuya mabouya* (p. 208)
17. Animales pequeños (longitud total menor de 200 mm); escamas ventrales medianas lisas; hocico puntiagudo; mancha negra con el centro claro sobre la unión del brazo *Neusticurus ecpleopus* (p. 218)
- Animales grandes (longitud total hasta 850 mm); escamas ventrales medianas ligeramente quilladas; hocico redondo sin mancha negra sobre la unión del brazo *Dracaena guianensis* (p. 214)
18. Escamas dorsales granulares más pequeñas que las ventrales (Fig. 33b) 19
- Escamas dorsales no granulares tan grandes como o sólo ligeramente más pequeñas que las ventrales 21
19. Más de 20 hileras de escamas ventrales longitudinales; escamas dorsales lisas *Tupinambis tequixin* (p. 223)
- Menos de 17 hileras de escamas ventrales longitudinales; gránulos dorsales pequeños, redondos o quillados 20
20. Escamas ventrales quilladas *Kentropyx pelviceps* (p. 215)
- Escamas ventrales lisas *Ameiva ameiva petersii* (p. 210)
21. Extremidades posteriores normales 22
- Extremidades posteriores reducidas a pequeñas yemas *Bachia trisanale trisanale* (p. 213)
22. Escamas dorsales lisas 23
- Escamas dorsales quilladas 24
23. Todas las escamas dorsales del cuerpo casi del mismo tamaño (Fig. 33c) *Mabuya mabouya* (p. 208)

Dorsum with two longitudinal rows of greatly enlarged scales (Fig. 33d)

..... *Iphisa elegans* (p. 215)

24. Scales around body in distinct transverse rows (Fig. 34a) 25

Scales around body not in distinct transverse rows (Fig. 34b) 28

25. Distinct lateral zone of granular scales between dorsals and ventrals (Fig. 34c) 26

Dorsal scales meeting or nearly meeting ventrals; no more than two longitudinal rows of granules laterally 27

Dorso con dos hileras de escamas longitudinales considerablemente dilatadas (Fig. 33d)

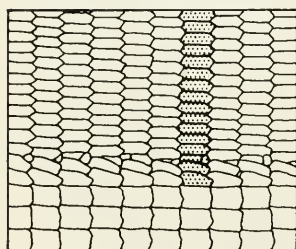
..... *Iphisa elegans* (p. 215)

24. Escamas alrededor del cuerpo en hileras transversales regulares (Fig. 34a) 25

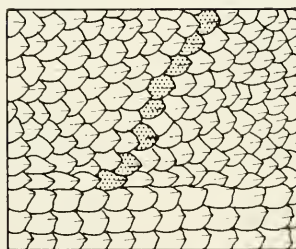
Escamas alrededor del cuerpo no en hileras transversales (Fig. 34b) .. 28

25. Zona lateral distinta de escamas granulares entre las dorsales y ventrales (Fig. 34c) 26

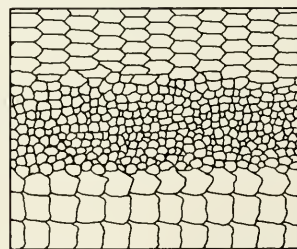
Escamas dorsales en contacto o casi en contacto con las ventrales; no más de dos hileras longitudinales de gránulos lateralmente 27



a



b



c

FIG. 34.—Lateral views of midbody scutellation (anterior to left): A. *Arthrosaura reticulata* with scales in transverse rows, B. *Leposoma parietale* with scales in diagonal rows, C. *Prionodactylus argulus* with granular lateral scales.

26. Frontonasal single (Fig. 35a); flanks uniform dark brown; white ventrolateral stripe extending from lip to hind limb

..... *Prionodactylus manicatus* (p. 221)

Frontonasal longitudinally divided (Fig. 35b); flanks brown with light-centered ocelli; ventrolateral stripe absent or indistinct

..... *Prionodactylus argulus* (p. 220)

26. Frontonasal entero (Fig. 35a); flancos uniformemente marrón oscuro; cinta ventrolateral blanca extendiéndose desde el labio hasta la extremidad posterior

..... *Prionodactylus manicatus* (p. 221)

Frontonasal dividido longitudinalmente (Fig. 35b); flancos marrones con ocelos más claros en el centro; cinta ventrolateral ausente o indistinta

..... *Prionodactylus argulus* (p. 220)

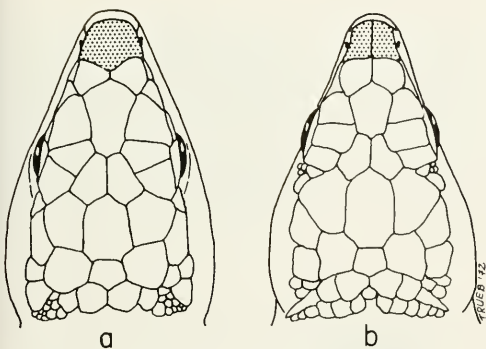


FIG. 35.—Dorsal views of heads: A. *Prionodactylus manicatus* with single frontonasal (stippled), B. *Prionodactylus argulus* with divided frontonasal (stippled).

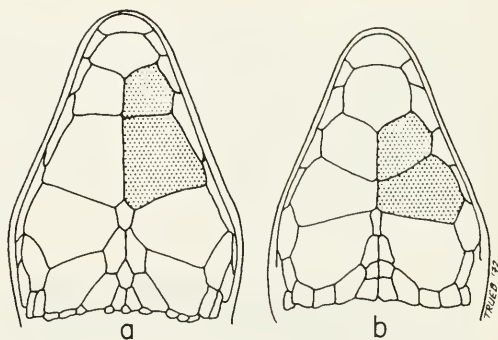


FIG. 36.—Ventral views of chins showing relative lengths of chinshields (stippled): A. *Arthrosaura reticulata*, B. *Ptychoglossus brevifrontalis*.

27. Three supraoculars; suture between second pair of chinshields much longer than suture between first pair (Fig. 36a); dorsal caudal scales weakly keeled, keels not extending posteriorly beyond margins of scales *Arthrosaura reticulata* (p. 213)

Four supraoculars; suture between second pair of chinshields shorter than suture between first pair (Fig. 36b); caudal scales moderately keeled, keels extending posteriorly beyond margins of scales

..... *Ptychoglossus brevifrontalis* (p. 222)

28. Ventral scales keeled 29

Ventral scales smooth
..... *Alopoglossus copii* (p. 210)

29. Head scales having a few rounded ridges; venter cream, becoming black in adult males
..... *Alopoglossus atriventris* (p. 209)

Head scales having many keels; venter cream or orange
..... *Leposoma parietale* (p. 217)

27. Tres supraoculares; sutura entre el segundo par de escudos mentales mucho más grande que la sutura entre el primer par (Fig. 36a); escamas dorsales caudales ligeramente quilladas, las quillas no sobrepasan los márgenes posteriores de las escamas
..... *Arthrosaura reticulata* (p. 213)

Cuatro supraoculares; sutura entre el segundo par de escudos mentales más corto que la sutura entre el primer par (Fig. 36b); escamas caudales ligeramente quilladas, las quillas sobrepasan los márgenes posteriores de las escamas
..... *Ptychoglossus brevifrontalis* (p. 222)

28. Escamas ventrales quilladas 29

Escamas ventrales lisas
..... *Alopoglossus copii* (p. 210)

29. Escamas cefálicas con pocas crestas redondas; vientre crema, negro en los machos adultos
..... *Alopoglossus atriventris* (p. 209)

Escamas cefálicas con muchas quillas; vientre crema o anaranjado
..... *Leposoma parietale* (p. 219)

KEY TO THE SNAKES

CLAVE DE LAS CULEBRAS

1. A deep pit between nostril and eye
(Fig. 37a) 2
- No deep pit between nostril and eye
(Fig. 37b) 5

1. Una fosa profunda entre el nostrilo
y el ojo (Fig. 37a) 2
- Sin fosa profunda entre el nostrilo
y el ojo (Fig. 37b) 5

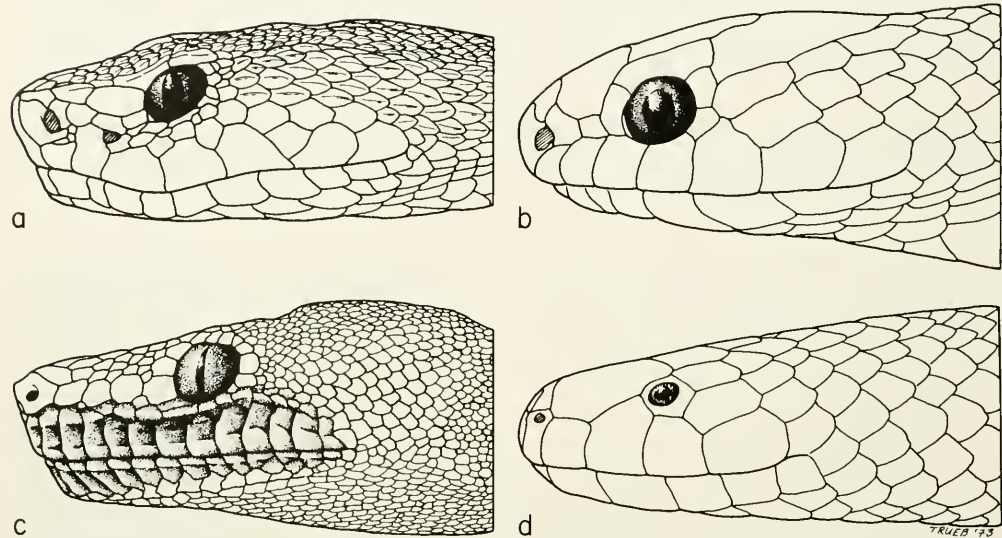


FIG. 37.—Sides of heads: A. *Bothrops atrox* with facial pit (stippled) between eye and nostril, B. *Clelia clelia* with normal colubrid scutellation, C. *Corallus caninus* with labial pits (stippled), D. *Anilius scytale* with eye beneath single scale.

2. All dorsal scales uniformly keeled
(Fig. 38a); two rows of scales between orbit and upper labials 3
- Scales in middorsal rows having knobby keels (Fig. 38e); four or five rows of scales between orbit and upper labials
..... *Lachesis muta muta* (p. 265)
3. Dorsum green with cream or yellow stripe on first row of dorsal scales
..... *Bothrops bilineatus smaragdinus* (p. 264)
- Dorsum with brown or black blotches; no yellow stripe of first row of dorsal scales 4

2. Todas las escamas dorsales uniformemente quilladas (Fig. 38a); dos hileras de escamas entre la órbita y las supralabiales 3
- Escamas de las hileras media dorsales con quillas nudosas (Fig. 38e); cuatro o cinco hileras de escamas entre la órbita y las supralabiales
..... *Lachesis muta muta* (p. 265)
3. Dorso verdoso con raya crema o amarilla en la primera hilera de escamas dorsales
..... *Bothrops bilineatus smaragdinus* (p. 264)
- Dorso con manchas marrones o negras sin raya amarilla en la primera hilera de las escamas dorsales 4

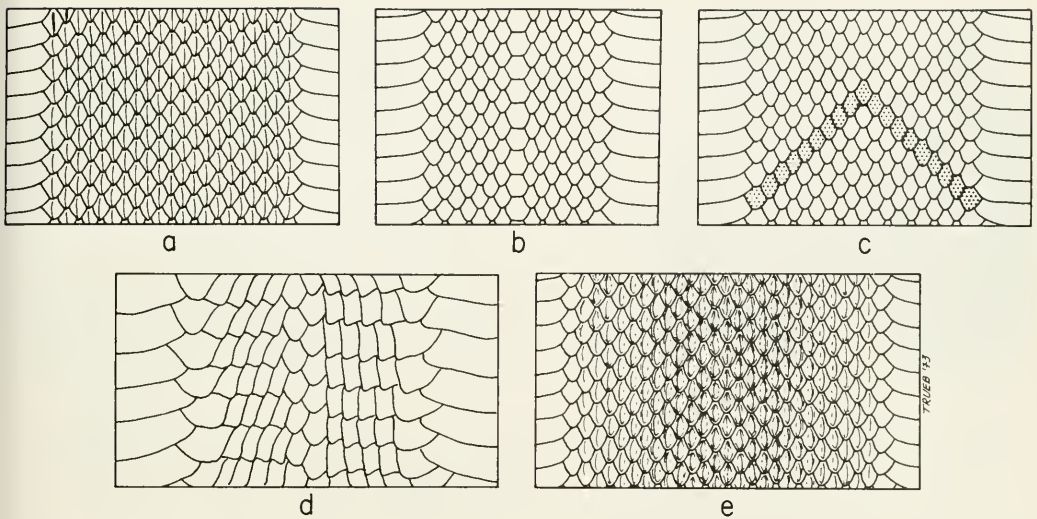


FIG. 38.—Dorsal scales of midbody: A. *Bothrops atrox* with uniformly keeled scales, B. *Imantodes cenchoa* with enlarged middorsal row; C. *Clelia clelia* with smooth scales (method of counting dorsal scales stippled), D. *Chironius carinatus* with scales in even-numbered oblique rows, E. *Lachesis muta* with knob-like middorsal scales.

4. Dorsum greenish yellow with narrow chocolate brown blotches; venter dark brown with yellow flecks *Bothrops castelnaudi* (p. 264)
 Dorsum tan, brown, or gray with large darker rhomboidal blotches; venter mottled cream and brown or black *Bothrops tarox* (p. 262)
4. Dorso amarillo verdoso con manchas angostas marrón chocolate; vientre marrón oscuro con moteados amarillos *Bothrops castelnaudi* (p. 264)
 Dorso bronceado, marrón o gris con grandes manchas romboidales oscuras; vientre moteado de crema y marrón o negro *Bothrops atrox* (p. 262)
5. Dorsal scales in more than 40 rows at midbody; top of head covered with many small scales (Fig. 39a); large scales present or not on snout (Fig. 39b) 6
 Dorsal scales in fewer than 30 rows at midbody; top of head covered with large plates (Fig. 39c) 10
5. Más de 40 hileras de escamas dorsales en medio del cuerpo; parte superior de la cabeza cubierta con muchas escamas pequeñas (Fig. 39a); escamas grandes presentes o no en el hocico (Fig. 39b) 6
 Menos de 30 hileras de escamas dorsales en medio del cuerpo; parte superior de la cabeza cubierta con placas grandes (Fig. 39c) 10
6. Scales on top of snout small, same size as those on top of head (Fig. 39a); single median longitudinal dark stripe on top of head *Boa constrictor constrictor* (p. 225)
6. Escamas sobre el hocico pequeñas, del mismo tamaño que aquellas sobre la cabeza (Fig. 39a); raya media longitudinal oscura sencilla sobre la cabeza *Boa constrictor constrictor* (p. 225)

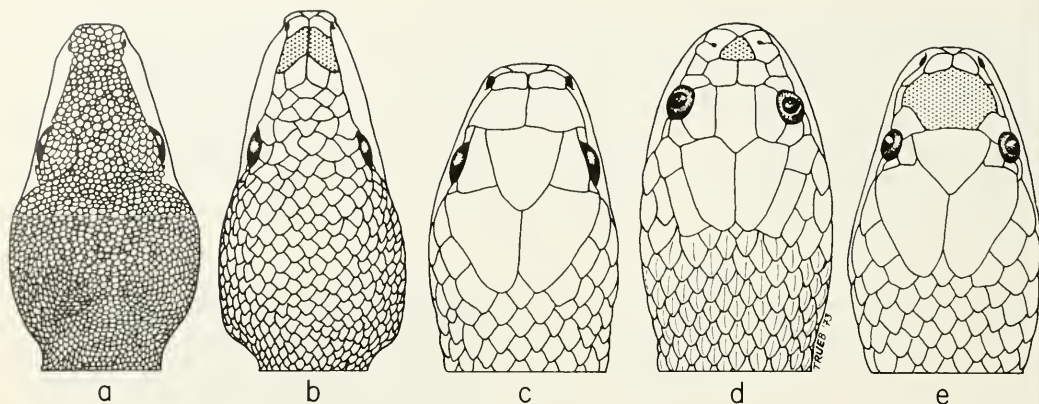


FIG. 39.—Tops of heads: A. *Boa constrictor* with uniformly small scales, B. *Epicrates cenchria* with small scales and enlarged internasals (stippled), C. *Clelia clelia* with normal colubrid scutellation, D. *Helicops angulatus* with single internasal (stippled), E. *Xenopholis scalaris* with single prefrontal (stippled).

- | | |
|--|--|
| <p>Scales on top of snout consisting minimally of one pair of enlarged internasals (Fig. 39b); dorsal head pattern not as described 7</p> | <p>Escamas sobre el hocico reducidas a un par de internasales grandes (Fig. 39b); diseño cefálico dorsal diferente a lo descrito 7</p> |
| <p>7. No pits in labials; top of head dark brown with broad tan or orange postorbital stripe
 <i>Eunectes murinus murinus</i> (p. 227)
 Pits present in labials (Fig. 37c); dorsal head pattern not as described 8</p> | <p>7. Sin fosa en las labiales; sobre la cabeza marrón oscuro con raya postorbital ancha bronceada o anaranjada
 <i>Eunectes murinus murinus</i> (p. 227)
 Fosas presentes en las labiales (Fig. 37c); diseño cefálico dorsal no como el descrito 8</p> |
| <p>8. Upper labials entering orbit; paired internasals bordered posteriorly by large scales (Fig. 39b); one loreal; dorsal head pattern consisting of narrow median and postorbital dark stripes; dorsal body pattern consisting of black circles with brown centers
 <i>Epicrates cenchria cenchria</i> (p. 226)
 Upper labials separated from orbit; paired internasals bordered posteriorly by small scales; two or more loreals; coloration not as described 9</p> | <p>8. Supralabiales en contacto con la órbita; internasales pareadas, bordeadas posteriormente por escamas grandes (Fig. 39b); una loreal; diseño cefálico dorsal compuesto de rayas medias angostas y postorbitales oscuras; diseño dorsal del cuerpo con círculos negros con rayas marrones
 <i>Epicrates cenchria cenchria</i> (p. 226)
 Supralabiales separadas de la órbita; internasales pareadas, bordeadas posteriormente por escamas pequeñas; dos o más loreales; coloración diferente a la descrita 9</p> |

9. Dorsal scales in fewer than 55 rows; two or three loreals; one preocular; nasals in contact medially; internasals large; pits absent in anterior upper labials; body brown or gray with dark brown or black saddles bordered by cream *Corallus enydris enydris* (p. 226)
- Dorsal scales in more than 55 rows; four loreals; two or three preoculars; nasals broadly separated by small internasals; pits present in all upper labials; body red or yellow in juveniles, green in adults, with narrow vertical white bars *Corallus caninus* (p. 225)
10. Ventral scales much wider than long; eye bordered by at least four scales; minimally six dorsal head shields (Fig. 39c) 11
- Ventral scales only slightly wider than long; eye contained in a single large scale (Fig. 37d); enlarged head shields consisting of small paired internasals, large paired prefrontals, and small diamond-shaped frontal *Anilius scytale scytale* (p. 224)
11. Dorsal scales in even number of rows (Fig. 38d) 12
- Dorsal scales in odd number of rows (Fig. 38c) 15
12. Dorsal scales in 12 rows anterior to midbody; anal plate divided (Fig. 40a) 13
- Dorsal scales in 10 rows anterior to midbody; anal plate single (Fig. 40b) 14
9. Menos de 55 hileras de escamas dorsales; dos o tres loreales; una preocular; nasales en contacto en la línea media; internasales grandes; fosas ausentes en la parte anterior de las supralabiales; cuerpo marrón o gris con dibujos en forma de montura de color marrón oscuro o negro bordeadas de crema *Corallus enydris enydris* (p. 226)
- Más de 55 hileras de escamas dorsales; cuatro loreales; dos o tres preoculares; nasales separadas por internasales pequeñas; fosas presentes en todas las supralabiales; cuerpo rojo o amarillo en juveniles, verde en los adultos, con barras angostas verticales blancas *Corallus caninus* (p. 225)
10. Escamas ventrales mucho más anchas que largas; ojo bordeado al menos por cuatro escamas; seis escudos sobre la cabeza como mínimo (Fig. 39c) 11
- Escamas ventrales sólo ligeramente más anchas que largas; ojo bordeado por una sola escama grande (Fig. 37d); escudos sobre la cabeza formados por las internasales pareadas pequeñas, prefrontales pareadas grandes, y frontal pequeña en forma del diamante *Anilius scytale scytale* (p. 224)
11. Escamas dorsales en hileras pares (Fig. 38d) 12
- Escamas dorsales en hileras impares (Fig. 38c) 15
12. Doce hileras de escamas dorsales en la parte anterior al media cuerpo; placa anal dividida (Fig. 40a) 13
- Diez hileras de escamas dorsales en la parte anterior al media cuerpo; placa anal entera (Fig. 40b) 14

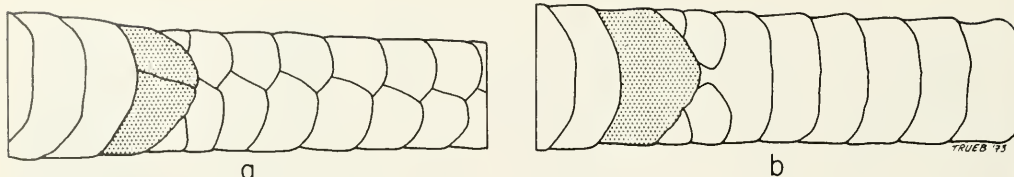


FIG. 40.—Ventral views of anal regions: A. *Leptodeira annulata* with divided anal plate (stippled) and divided subcaudals, B. *Pseudoboa coronata* with single anal plate (stippled) and single subcaudals.

- | | |
|---|---|
| <p>13. Ventrals fewer than 155
 <i>Chironius carinatus</i> (p. 231)</p> <p>Ventrals more than 155
 <i>Chironius multiventris</i> (p. 233)</p> | <p>13. Menos de 155 ventrales
 <i>Chironius carinatus</i> (p. 231)</p> <p>Más de 155 ventrales
 <i>Chironius multiventris</i> (p. 233)</p> |
| <p>14. Paravertebral rows of scales keeled (weakly or not at all in juveniles); ventrals fewer than 155; caudals more than 117; juveniles grayish tan with olive-brown transverse blotches; adults olive-brown; venter yellow anteriorly
 <i>Chironius fuscus</i> (p. 232)</p> <p>Paravertebral rows of scales smooth; ventrals more than 150; caudals fewer than 118; juveniles green above and below; adults black or dark olive-brown with rust or orange spots; venter rust or orange-tan anteriorly
 <i>Chironius scurrulus</i> (p. 234)</p> | <p>14. Hileras de escamas paravertebrales quilladas (poco notorio en juveniles); menos de 155 ventrales; más de 117 caudales; juveniles, bronceado-grisáceos con rayas transversales marrón-oliva; vientre amarillo anteriormente
 <i>Chironius fuscus</i> (p. 232)</p> <p>Hileras de escamas paravertebrales lisas; más de 150 ventrales; menos de 118 caudales; juveniles, verde arriba y abajo; adultos, negros o marrón-oliva oscuro con manchas marrón-rojizas o anaranjadas; vientre marrón-rojizas anaranjado-bronceado anteriormente
 <i>Chironius scurrulus</i> (p. 234)</p> |
| <p>15. Some or all dorsal scales keeled (Fig. 38a) 16</p> <p>All dorsal scales smooth (Fig. 38c) 21</p> | <p>15. Algunas o todas las escamas dorsales quilladas (Fig. 38a) 16</p> <p>Todas las escamas dorsales lisas (Fig. 38c) 21</p> |
| <p>16. Internasals paired; nostrils directed laterally (Fig. 39c) 17</p> <p>Internasals fused into single scale; nostrils directed dorsolaterally (Fig. 39d) 20</p> | <p>16. Internasales pareadas; nostrilos orientados lateralmente (Fig. 39c) 17</p> <p>Internasales fusionadas en una sola escama; nostrilos orientados dorsolateralmente (Fig. 39d) 20</p> |
| <p>17. Dorsal scales in 17 rows at midbody 18</p> | <p>17. 17 hileras de escamas dorsales a medio cuerpo 18</p> |

- Dorsal scales in 21 rows at midbody 19
18. Anal plate single (Fig. 40b)
Dendrophidion dendrophis (p. 236)
- Anal plate divided (Fig. 40a)
Drymobius rhombifer (p. 240)
19. Dorsal scales in 12 to 15 rows one head length anterior to anus; loreal quadrangular; one preocular; head and body dull olive-tan; no contrasting pale band across head
Pseustes sulphureus sulphureus (p. 255)
- Dorsal scales in 21 rows one head length anterior to anus; loreal elongate; no preocular; uniform dark gray with pale band across head
Ninia hudsoni (p. 250)
20. Dorsal scales in 19 rows at midbody
Helicops angulatus (p. 242)
- Dorsal scales in 21 rows at midbody
Helicops petersi (p. 243)
21. Vertebral scale row noticeably wider than other rows at midbody (Fig. 38b); body slender, laterally compressed; pupil vertically elliptical 22
- Vertical scale row same width as others at midbody (Fig. 38c), or, if wider, body pattern not consisting of blotches; body not laterally compressed; pupil round 28
22. Dorsal scales in 13 rows at midbody 23
- Dorsal scales in 15 or more rows at midbody 25
- 21 hileras de escamas dorsales a medio cuerpo 19
18. Placa anal entera (Fig. 40b)
Dendrophidion dendrophis (p. 236)
- Placa anal dividida (Fig. 40a)
Drymobius rhombifer (p. 240)
19. De 12 a 15 hileras de escamas dorsales a una distancia de una cabeza de largo anterior al ano; loreal cuadrangular; una preocular; cabeza y cuello bronceado-oliva opaco; sin contraste de banda pálida sobre la cabeza
Pseustes sulphureus sulphureus (p. 255)
- 21 hileras de escamas dorsales a una distancia de una cabeza de largo anterior al ano; loreal alargada; sin preocular; gris oscuro uniforme con una banda pálida sobre la cabeza
Ninia hudsoni (p. 250)
20. 19 hileras de escamas dorsales a medio cuerpo
Helicops angulatus (p. 242)
- 21 hileras de escamas dorsales a medio cuerpo
Helicops petersi (p. 243)
21. La hilera de escamas vertebrales notablemente más ancha que las otras hileras a medio cuerpo (Fig. 38b); cuerpo delgado, lateralmente comprimido; pupila vertical elíptica 22
- La hilera de escamas vertebrales de igual anchura que las otras en medio del cuerpo (Fig. 38c); o si más anchas el cuerpo, carece de manchas; cuerpo no comprimido lateralmente; pupila redonda 28
22. 13 hileras de escamas dorsales a medio cuerpo 23
- 15 o más hileras de escamas dorsales a medio cuerpo 25

23. Loreal present (Fig. 41a)
..... *Dipsas catesbyi* (p. 237)

Loreal absent (Fig. 41b-c) 24

23. Loreal presente (Fig. 41a)
..... *Dipsas catesbyi* (p. 237)

Loreal ausente (Fig. 41b, c) 24

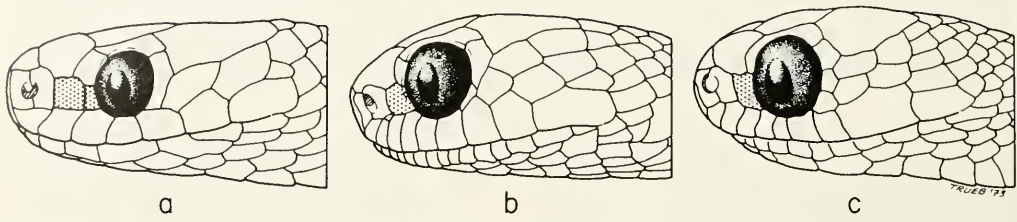


FIG. 41.—Lateral views of heads showing loreal and preocular scales (stippled): A. *Dipsas catesbyi*, B. *Dipsas indica*, C. *Dipsas pavonina*.

24. Top of head brown with dark brown streaks; body tan or gray with dark brown blotches wider ventrally than dorsally; venter dark brown with cream ventrolateral spots
..... *Dipsas indica ecuadorensis* (p. 238)

Top of head black with white transverse line on snout; body brown with broad black blotches wider dorsally than ventrally; posterior venter uniform tan
..... *Dipsas pavonina* (p. 239)

24. Parte superior de la cabeza marrón con rayas marrón-oscuras; cuerpo bronceado o gris con manchas marrón oscuras más anchas en el vientre que en el dorso; vientre marrón-oscuro con manchas ventrolaterales crema
..... *Dipsas indica ecuadorensis*
..... (p. 238)

Parte superior de la cabeza negra con línea transversal blanca sobre el hocico; cuerpo marrón con manchas negras dilatadas más anchas en el dorso que ventralmente; vientre uniforme bronceado posteriormente
..... *Dipsas pavonina* (p. 239)
25. Dorsal scales in 15 rows at midbody
..... *Imantodes lentiferus* (p. 245)

Dorsal scales in 17 or more rows at midbody 26

25. 15 hileras de escamas dorsales a medio cuerpo
..... *Imantodes lentiferus* (p. 245)

17 o más hileras de escamas dorsales a medio cuerpo 26
26. Dorsal scales in 17 rows at midbody
..... *Imantodes cenchoa cenchoa* (p. 244)

Dorsal scales in 19 rows at midbody 27

26. 17 hileras de escamas dorsales a medio cuerpo
..... *Imantodes cenchoa cenchoa* (p. 244)

19 hileras de escamas dorsales a medio cuerpo 27

27. Anal plate divided (Fig. 40a); one anterior temporal (Fig. 42a); body blotches extending laterally to fourth or fifth row of scales
 *Leptodeira annulata annulata*
 (p. 247)

Anal plate single (Fig. 40b); two anterior temporals (Fig. 42b); body pattern consisting of narrow dark crossbars extending laterally to first or second row of scales
 *Tripanurgos compressus* (p. 258)

27. Placa anal dividida (Fig. 40a); una temporal anterior (Fig. 42a); manchas corporales extendidas lateralmente hasta la cuarta o quinta hilera de escamas
 *Leptodeira annulata annulata*
 (p. 247)

Placa anal entera (Fig. 40b); dos temporales anteriores (Fig. 42b); diseño del cuerpo formado por barras transversales oscuras extendidas lateralmente hasta la primera o segunda hilera de escamas
 *Tripanurgos compressus* (p. 258)

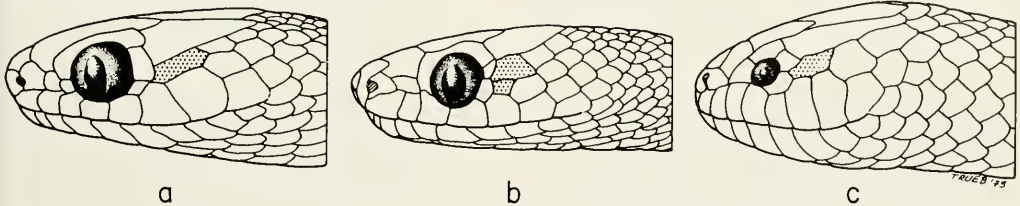


FIG. 42.—Lateral views of heads showing number and position of anterior temporals (stippled): A. *Leptodeira annulata*, B. *Tripanurgos compressus*, C. *Micrurus surinamensis*.

28. Dorsal scales in 15 rows at midbody 29

 Dorsal scales in 17 or more rows at midbody 40

29. Color pattern consisting of red and black rings completely encircling body, or at least evident ventrally; yellow or white rings present or not 30

 Color pattern not consisting of red and black rings encircling body .. 35

30. Anal plate single (Fig. 40a); one pair of chinshields; one postocular (Fig. 43b) .. *Atractus elaps* (p. 227)

 Anal plate divided (Fig. 40a); two pairs of chinshields; two postoculars (Fig. 43a) 31

28. 15 hileras de escamas dorsales a medio cuerpo 29

 17 o más hileras de escamas dorsales a medio cuerpo 40

29. Diseño de coloración consiste de anillos rojos y negros circundando completamente el cuerpo, o al menos ventralmente evidentes; anillos amarillos o blancos presentes o no 30

 Diseño de coloración diferente a la descrita 35

30. Placa anal entera (Fig. 40b); un par de placas mentales; una postocular (Fig. 43b)
 *Atractus elaps* (p. 227)

 Placa anal dividida (Fig. 40a); dos pares de placas mentales; dos postoculares (Fig. 43a) 31

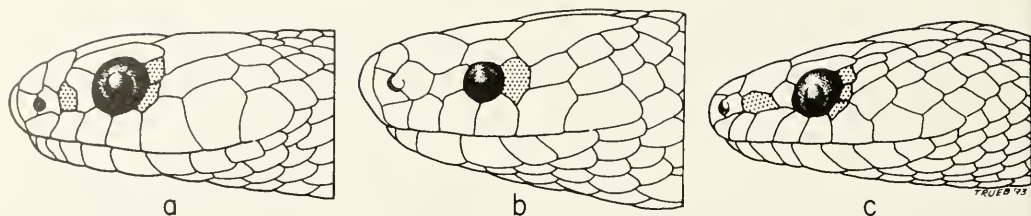


FIG. 43.—Lateral views of heads showing loreal (stippled) between nasal and preocular or orbit and number of postoculars (stippled): A. *Erythrolamprus aesculapii*, B. *Atractus elaps*, C. *Siphiophis cervinus*.

31. Two pairs of secondary temporals (Fig. 42a) *Erythrolamprus aesculapii aesculapii* (p. 242)

One pair of secondary temporals (Fig. 42c) 32

32. Head broad, depressed; nostrils directed dorsally; eye small; fourth upper labial barely entering orbit; frontal small; head shields black with reddish brown mark on each scale *Micrurus surinamensis surinamensis* (p. 262)

Head not depressed; nostrils directed laterally; eye normal; fourth upper labial broadly entering orbit; frontal large; head pattern not as described 33

33. Black rings in triads (red-black-yellow-black-yellow-black-red) 34

Black rings not in triads; 36-38 black rings, incompletely separated from red rings by white scales, on body

Micrurus langsdorffi langsdorffi (p. 260)

34. Snout black; yellow band anterior to eyes; posterior part of head and neck red; yellow rings on body much narrower than black rings; scales in

31. Dos pares de temporales secundarias (Fig. 42a) *Erythrolamprus aesculapii aesculapii* (p. 242)

Un par de temporales secundarias (Fig. 42c) 32

32. Cabeza ancha, deprimida; nostrilos orientadas dorsalmente; ojo pequeño; cuarta supralabial escasamente entra en la órbita; frontal pequeña; escudos de la cabeza negros con una marca marrón rojiza en cada escama *Micrurus surinamensis surinamensis* (p. 262)

Cabeza no deprimida, nostrilos orientados lateralmente; ojo normal; cuarta supralabial penetra bien en la órbita; frontal grande; diseños cefálicos diferentes a los descritos arriba 33

33. Anillos negros en tríadas (rojo-negro-amarillo-negro-amarillo-negro-rojo) 34

Anillos negros no en tríadas; 36-38 anillos negros incompletamente separados de los anillos rojos por escamas blancas en el cuerpo

Micrurus langsdorffi langsdorffi (p. 260)

34. Hocico negro; una banda amarilla anterior a los ojos; parte posterior de la cabeza y el cuello rojos; los anillos amarillos del cuerpo más angostos

- red areas not or barely tipped with black
 --- *Micrurus lemniscatus helleri*
 (p. 261)
- Snout and top of head black; no yellow band anterior to eyes; nape black; yellow rings on body nearly as wide as black rings; scales in red and yellow rings heavily tipped with black
 --- *Micrurus spixii obscurus* (p. 261)
35. Anal plate divided (Fig. 40a) 36
 Anal plate single (Fig. 40b) 37
36. Head black with broad yellow band posterior to eye; dorsum and venter of body black with large orange or red (yellow in preservative) spots on venter
 --- *Leptomicrurus narducii* (p. 260)
 Coloration not as described 38
37. Dorsal scales in 15 rows one head length anterior to anus; dorsum brown with narrow black stripes; head brown *Tantilla melanocephala melanocephala*
 (p. 256)
 Dorsal scales in 11 to 13 rows one head length anterior to anus; dorsum green with coppery tint laterally; head green with scales bordered by black *Leptophis ahuetulla nigromarginatus* (p. 249)
38. Loreal absent (Fig. 43b); head and neck black with broad cream band across head; dorsum of body red with scales tipped with black
 *Drepanoides anomalus* (p. 240)
- que los anillos negros; escamas de las áreas rojas sin o con pocos puntos negros
 --- *Micrurus lemniscatus helleri*
 (p. 261)
- Hocico y parte superior de la cabeza negros; ninguna banda amarilla anterior a los ojos; nuca negra; anillos amarillos del cuerpo casi tan anchos como los anillos negros; escamas de los anillos rojos y amarillos profusamente punteados de negro
 --- *Micrurus spixii obscurus* (p. 261)
35. Placa anal dividida (Fig. 40a) 36
 Placa anal entera (Fig. 40b) 37
36. Cabeza negra con banda ancha amarilla posterior al ojo; dorso y vientre del cuerpo negros con manchas grandes anaranjadas o rojas (amarillo en preservativo)
 --- *Leptomicrurus narducii* (p. 260)
 Coloración diferente a la descrita 38
37. 15 hileras de escamas dorsales a una distancia de una cabeza de longitud anterior al ano; dorso marrón con rayas negras angostas; cabeza marrón
 --- *Tantilla melanocephala melanocephala*
 (p. 256)
 De 11 a 13 hileras de escamas dorsales a una distancia de una cabeza de longitud anterior al ano; dorso verde con tinte cuproso lateralmente; cabeza verde con escamas bordeadas de negro
 --- *Leptophis ahuetulla nigromarginata*
 (p. 249)
38. Loreal ausente (Fig. 43b); cabeza y cuello negros con banda crema ancha sobre la cabeza; dorso del cuerpo rojo con escamas punteadas de negro
 --- *Drepanoides anomalus* (p. 240)

- Loreal present (Fig. 43a); coloration not as described 39
39. Nuchal collar absent; dorsum black in adults, gray with brown blotches in juveniles
Drymoluber dichrous (p. 241)
 Pale nuchal collar present; dorsum gray or brown with or without tan spots laterally; venter gray, or cream with midventral brown spots
Atractus occipitoalbus (p. 230)
40. Dorsal scales in 17 rows at midbody 41
 Dorsal scales in 19 or 21 rows at midbody 48
41. Anal plate divided (Fig. 40a) 42
 Anal plate single (Fig. 40b) 45
42. Color pattern consisting of dark blotches or rings completely encircling body
Liophis cobella (p. 250)
 Color pattern consisting of stripes, at least on tail, or unicolor dorsally 43
43. Dorsal pattern consisting of distinct dark brown and tan stripes; mid-venter immaculate cream
Rhadinaea brevirostris (p. 255)
 Stripes, if present, consisting of lateral black stripe posteriorly; venter usually marked with black squares 44
44. Border of upper lip dark, delimiting white labial stripe; dark pattern on chin; ventrals more than 150
Leimadophis sp. (p. 247)
 Border of upper lip pale; no white labial stripe; chin immaculate; ventrals fewer than 150
Leimadophis reginae (p. 246)
- Loreal presente (Fig. 43a); coloración diferente a la descrita 39
39. Collar nuchal ausente; dorso negro en los adultos, gris con rayas marrones en los juveniles
Drymoluber dichrous (p. 241)
 Collar nuchal pálido presente; dorso gris o marrón con o sin manchas bronceadas laterales; vientre gris o crema con manchas medioventrales marrones
Atractus occipitoalbus (p. 230)
40. 17 hileras de escamas dorsales a medio cuerpo 41
 19 o 21 hileras de escamas dorsales a medio cuerpo 48
41. Placa anal dividida (Fig. 40a) 42
 Placa anal entera (Fig. 40b) 45
42. Diseño de coloración consiste de manchas oscuras o anillos circundando completamente el cuerpo
Liophis cobella (p. 250)
 Diseño de coloración consiste de rayas, al menos en la cola; o unicolor dorsalmente 43
43. Diseño dorsal compuesto de cintas marrón oscuras bronceadas distintas; vientre crema immaculado en la línea media
Rhadinaea brevirostris (p. 255)
 Cintas cuando presentes compuestas de rayas laterales negras posteriormente; vientre usualmente marcado con cuadrados negros 44
44. Borde supralabial oscuro, limitado por una raya labial blanca; diseño oscuro sobre el mentón; más de 150 ventrales *Leimadophis* sp. (p. 247)
 Borde supralabial pálido; sin raya supralabial blanca; mentón immaculado; menos de 150 ventrales
Leimadophis reginae (p. 246)

45. Prefrontals fused into a single scale (Fig. 39e)
 Xenopholis scalaris (p. 260)
 Prefrontals paired (Fig. 39c) 46
46. Subcaudals single (Fig. 40b); head black; body red above (tips of scales black in large adults), cream below
 Pseudoboa coronata (p. 255)
 Subcaudals divided (Fig. 40a) 47
47. Body slender; head pointed; loreal absent (Fig. 43b); preocular present; coloration consisting of brown and green stripes
 Oxybelis argenteus (p. 251)
 Body robust; head rounded; loreal present, elongate; preocular absent; coloration consisting of dark brown blotches
 Atractus major (p. 229)
48. Dorsal scales in 21 rows; anal plate divided (Fig. 40a); one anterior temporal (Fig. 42a)
 Xenodon severus (p. 258)
 Dorsal scales in 19 rows; anal plate single (Fig. 40b); two anterior temporals (Fig. 42b) 49
49. Two or three postoculars (Fig. 43c); color pattern consisting of more than 60 irregular transverse black bars
 Siphlophis cervinus (p. 256)
 Two postoculars (Fig. 43a); color pattern on body uniform red or black, or with fewer than 40 wide black bands 50
50. Preocular not in contact with frontal (Fig. 39c) 51
 Preocular in contact with frontal 52
45. Prefrontales fusionadas en una sola escama (Fig. 39e)
 Xenopholis scalaris (p. 260)
 Prefrontales pareadas (Fig. 39c) 46
46. Subcaudales enteras (Fig. 40b); cabeza negra; cuerpo rojo arriba (con las puntas de las escamas negras en los adultos) crema abajo
 Pseudoboa coronata (p. 255)
 Subcaudales divididas (Fig. 40a) 47
47. Cuerpo delgado; cabeza puntuda; loreal ausente (Fig. 43b); preocular presente; coloración compuesta de rayas marrones y verdes
 Oxybelis argenteus (p. 251)
 Cuerpo robusto; cabeza redonda; loreal presente; alargada; preocular ausente; coloración compuesta de manchas marrón oscuras
 Atractus major (p. 229)
48. 21 hileras de escamas dorsales; placa anal dividida (Fig. 40a); una temporal anterior (Fig. 42a)
 Xenodon severus (p. 258)
 19 hileras de escamas dorsales; placa anal entera (Fig. 40b); dos temporales anteriores (Fig. 42b) 49
49. Dos o tres postoculares (Fig. 43c); diseño de coloración compuesto por 60 barras transversales irregulares negras
 Siphlophis cervinus (p. 256)
 Dos postoculares (Fig. 43a); diseño de coloración en el cuerpo rojo uniforme o negro, o con menos de 40 bandas anchas negras 50
50. Preocular no en contacto con la frontal (Fig. 39c) 51
 Preocular en contacto con la frontal 52

51. Ventrals more than 215
 Clelia clelia clelia (p. 235)
 Ventrals fewer than 215
 Oxyrhopus formosus (p. 253)

52. Color pattern consisting of narrow red or cream bands separated by broad black bands; subcaudals more than 97
 Oxyrhopus petola digitalis (p. 254)
 Color pattern consisting of broad black bands, narrower red bands, and much narrower cream bands, forming triads (red-black-cream-black-cream-black-red) posteriorly; subcaudals fewer than 97
 Oxyrhopus melanogenys (p. 253)

51. Más de 215 ventrales
 Clelia clelia clelia (p. 235)
 Menos de 215 ventrales
 Oxyrhopus formosus (p. 253)

52. El diseño de coloración consiste de bandas angostas rojas o crema separadas por bandas blancas anchas; más de 97 subcaudales
 Oxyrhopus petola digitalis (p. 254)
 El diseño de coloración consiste de bandas negras anchas, bandas rojas más angostas, y bandas cremas aún más angostas, formando tríadas (roja-negra-crema-negra-crema-negra-roja) posteriormente; menos de 97 subcaudales
 Oxyrhopus melanogenys (p. 253)

KEY TO THE KNOWN TADPOLES

1. Mouth terminal 2
 Mouth ventral or anteroventral (Fig. 44a) 17
 2. Lips protruding; (Fig. 44b), completely bordered by large, pointed papillae
 Ceratophrys cornuta (p. 85)
 Lips not protruding (Fig. 44c); at least upper lip lacking papillae 3
 3. Beaks and denticles absent (Fig. 45a); spiracles paired 4

CLAVE DE LOS RENACUAJOS CONOCIDOS

1. Boca terminal 2
 Boca ventral o anteroventral (Fig. 44a) 17
 2. Labios sobresalientes (Fig. 44b), completamente bordeados de papilas puntudas, grandes
 Ceratophrys cornuta (p. 85)
 Labios no sobresalientes (Fig. 44c); al menos el labio superior sin papilas 3
 3. Picos córneos y denticulos ausentes (Fig. 45a); espiráculos pareados ... 4

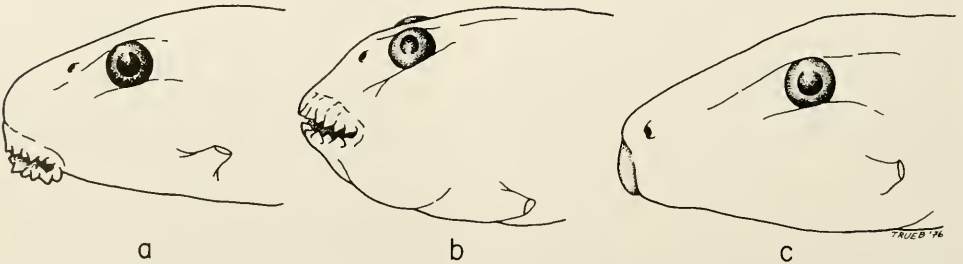


FIG. 44.—Lateral views of bodies of tadpoles: A. *Rana palmipes* with anteroventral mouth, B. *Ceratophrys cornuta* with terminal mouth and protruding lips, C. *Hyla leucophyllata* with terminal mouth and no protruding lips.

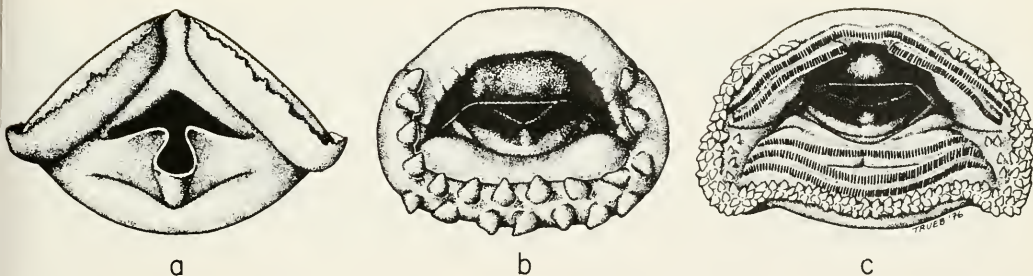


FIG. 45.—Mouths of tadpoles: A. *Hamptophryne boliviana* lacking beaks and denticles, B. *Hyla leucophyllata* with beaks but no denticles, C. *Phyllomedusa tarsius* with beaks and denticles.

- | | |
|--|---|
| Beaks present; denticles present or absent; spiracle single 5 | Picos córneos presentes; denticulos presentes o ausentes; espiráculo único 5 |
| 4. Body much wider than deep; caudal fins extending to tip of tail
..... <i>Hamptophryne boliviana</i> (p. 190) | 4. Cuerpo más ancho que alto; aletas caudales extendiéndose hasta el extremo de la cola
..... <i>Hamptophryne boliviana</i> (p. 190) |
| Body as deep as wide; caudal fins not extending to tip of tail
..... <i>Chiasmocleis anátipes</i> (p. 187) | Cuerpo tan alto como ancho; aletas caudales no se extienden hasta el extremo de la cola
..... <i>Chiasmocleis anátipes</i> (p. 187) |
| 5. Denticles absent (Fig. 45b); spiracle lateral 6 | 5. Denticulos ausentes (Fig. 45b); espiráculo lateral 6 |
| Denticles present (Fig. 45c); spiracle ventral 14 | Denticulos presentes (Fig. 45c); espiráculo ventral 14 |
| 6. Body in dorsal view violin-shaped (Fig. 46a) 7 | 6. Cuerpo, en vista dorsal, con forma de violín (Fig. 46a) 7 |
| Body in dorsal view ovoid (Fig. 46b) 10 | Cuerpo, en vista dorsal, con forma ovoidal (Fig. 46b) 10 |

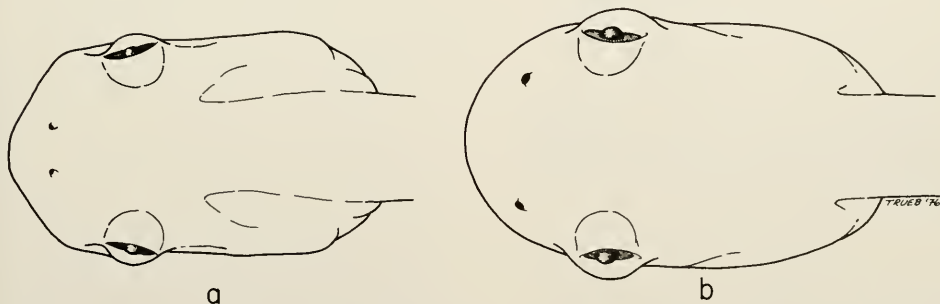


FIG. 46.—Dorsal views of tadpoles: A. *Hyla leucophyllata* (violin-shaped), B. *Hyla rubra* (ovoid).

7. Mouth bordered by fleshy fold laterally and ventrally; tail marked by two broad vertical black bars
 *Hyla triangulum* (p. 167)
- Mouth bordered by papillae laterally and ventrally; tail not marked by two broad black bars 8
8. Throat and belly metallic gold; dorsum gray to reddish brown; tail black or gray with black reticulations ... *Hyla sarayacuensis* (p. 165)
- Throat and belly striped black and white; dorsum tan or brown 9
9. Dorsum tan with black lateral stripe bordered below by metallic cream stripe; belly silvery white with three longitudinal black stripes
 *Hyla bifurca* (p. 130)
- Dorsum dark brown; flanks black; white lateral stripe extending from below eye to proximal part of tail; belly black with cream longitudinal dashes *Hyla leucophyllata*
 (p. 152)
10. Labial papillae absent; body and tail pale orange with brown flecks
 *Hyla rhodopepla* (p. 159)
- Labial papillae present; body and tail not so patterned 11
11. Tail terminating in a slender tip including fins (Fig. 47a); dorsum olive-tan with brown transverse marks; throat gray with brown flecks; tail tan with brown spots
 *Hyla marmorata* (p. 153)
- Tail terminating in a long filament beyond the fins (Fig. 47b); coloration not as described 12
7. Boca bordeada por ribete carnoso lateral y ventralmente; cola marcada por dos anchas barras verticales negras ... *Hyla triangulum* (p. 167)
- Boca bordeada por papilas lateral y ventralmente; cola sin barras verticales negras 8
8. Garganta y vientre amarillo-metálicos; dorso gris o café-rojizo; cola negra o gris con reticulaciones negras ... *Hyla sarayacuensis* (p. 165)
- Garganta y vientre con bandas blancas y negras; dorso marrón claro o marrón 9
9. Dorso marrón claro con banda lateral negra bordeada inferiormente por banda crema-metálica; vientre blanco-plateado con tres bandas negras longitudinales
 *Hyla bifurca* (p. 130)
- Dorso marrón oscuro; flancos negros; banda lateral blanca extendiéndose desde debajo del ojo hasta la parte proximal de la cola; vientre negro con líneas longitudinales cremas ... *Hyla leucophyllata*
 (p. 152)
10. Papilas labiales ausentes; cuerpo y cola anaranjado-pálidos con pecas marrones
 *Hyla rhodopepla* (p. 159)
- Papilas labiales presentes; cuerpo y cola diferente a lo descrito 11
11. Cola terminando en punta incluyendo las aletas (Fig. 47a); dorso marrón-oliva con marcas transversales marrones; garganta gris con pecas marrones; cola marrón claro con manchas marrones
 *Hyla marmorata* (p. 153)
- Cola terminando en un largo filamento por detrás de las aletas (Fig. 47b); coloración diferente a la descrita 12

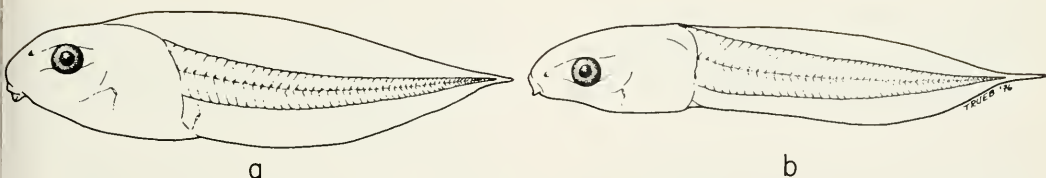


FIG. 47.—Lateral views of tadpoles: A. *Hyla rubra* with pointed tip of tail and dorsal fin extending onto body, B. *Hyla leucophyllata* with filamentous tail and dorsal fin not extending onto body.

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| <p>12. Body dark brown with cream transverse bar on snout and one on body posterior to eyes <i>Hyla parviceps</i> (p. 156)</p> <p>Body lacking transverse cream bars 13</p> <p>13. Body brown with two short yellowish tan longitudinal bars on snout; tail orange proximally, with gray vertical marks distally <i>Hyla bokermanni</i> (p. 133)</p> <p>Body brown with diffuse tan dorso-lateral stripe; tail tan with brown mottling and red streak on dorsal fin <i>Hyla brevifrons</i> (p. 135)</p> <p>14. Labial papillae in two rows laterally and ventrally 15</p> <p>Labial papillae in one row laterally and two rows ventrally 16</p> <p>15. Body and tail yellow with diffuse orange spot posteriorly on ventral fin <i>Phyllomedusa tomopterna</i> (p. 179)</p> <p>Body and tail olive green <i>Phyllomedusa vaillanti</i> (p. 180)</p> <p>16. Fins not extending to tip of tail; body and tail bluish gray <i>Phyllomedusa palliata</i> (p. 176)</p> <p>Fins extending to tip of tail; dorsum tan; flanks and tail green <i>Phyllomedusa tarsi</i> (p. 177)</p> | <p>12. Cuerpo marrón oscuro con barra transversal crema sobre el hocico y otra en el cuerpo posterior a los ojos <i>Hyla parviceps</i> (p. 156)</p> <p>Cuerpo sin barras transversales cremas 13</p> <p>13. Cuerpo marrón con dos barras longitudinales cortas de color marrón claro sobre el hocico; cola anaranjada proximalmente, con marcas verticales grises distalmente <i>Hyla bokermanni</i> (p. 133)</p> <p>Cuerpo marrón con banda difusa dorsolateral marrón clara; cola marrón clara con motas marrones y línea roja sobre la aleta dorsal <i>Hyla brevifrons</i> (p. 135)</p> <p>14. Papilas labiales en dos corridas lateral y ventralmente 15</p> <p>Papilas labiales en una corrida lateral y en dos ventralmente 16</p> <p>15. Cuerpo y cola amarillos con mancha posterior difusa anaranjada en la aleta ventral <i>Phyllomedusa tomopterna</i> (p. 179)</p> <p>Cuerpo y cola verde-oliva <i>Phyllomedusa vaillanti</i> (p. 180)</p> <p>16. Aletas sin extenderse hasta la punta de la cola; cuerpo y cola gris-azulados <i>Phyllomedusa palliata</i> (p. 176)</p> <p>Aletas extendiéndose hasta el extremo de la cola; dorso marrón claro; flancos y cola verdes <i>Phyllomedusa palliata</i> (p. 177)</p> |
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|---|--|
| <p>17. Three upper rows of denticles 18
 Fewer than three upper rows of
 denticles 19</p> <p>18. Five lower rows of denticles; body
 and tail black
 <i>Osteocephalus taurinus</i> (p. 172)</p> <p>Six lower rows of denticles; body
 brown; tail cream with dark brown
 stripes
 <i>Phrynohyas venulosa</i> (p. 174)</p> <p>19. Two upper rows of denticles 20
 Fewer than two upper rows of den-
 ticles 43</p> <p>20. Three lower rows of denticles 21
 Four lower rows of denticles 41</p> <p>21. Dorsal and ventral fins much deeper
 than caudal musculature at mid-
 length of tail; dorsal fin originating
 on dorsum of body 22</p> <p>Dorsal and ventral fins not, or only
 slightly, deeper than caudal muscu-
 lature at midlength of tail; dorsal fin
 not originating on dorsum of body
 26</p> <p>22. Lowermost row of denticles protrud-
 ing through lower lip
 <i>Hyla garbei</i> (p. 144)</p> <p>Lowermost row of denticles not pro-
 truding through lower lip 23</p> <p>23. Two rows of labial papillae laterally
 24</p> <p>One row of labial papillae laterally
 25</p> | <p>17. Tres filas superiores de denticulos
 18
 Menos de tres filas superiores de
 denticulos 19</p> <p>18. Cinco filas inferiores de denticulos;
 cuerpo y cola negra
 <i>Osteocephalus taurinus</i> (p. 172)</p> <p>Seis filas inferiores de denticulos;
 cuerpo marrón; cola crema con ban-
 das marrón oscuras
 <i>Phrynohyas venulosa</i> (p. 174)</p> <p>19. Dos filas superiores de denticulos
 20
 Menos de dos filas superiores de
 denticulos 43</p> <p>20. Tres filas inferiores de denticulos
 21
 Cuatro filas inferiores de denticulos
 41</p> <p>21. Aletas dorsales y ventrales más altas
 que la musculatura caudal en mitad
 de la cola; aleta dorsal originándose
 sobre el dorso del cuerpo 22</p> <p>Aletas dorsales y ventrales no más,
 o apenas más, altas que la muscu-
 latura caudal en mitad de la cola;
 aleta dorsal no originándose sobre
 el dorso del cuerpo 26</p> <p>22. La fila más inferior de denticulos en
 el labio inferior
 <i>Hyla garbei</i> (p. 144)</p> <p>La fila más inferior de denticulos no
 en el labio inferior 23</p> <p>23. Dos corridas de papilas labiales
 lateralmente 24</p> <p>Una corrida de papilas labiales lat-
 eralmente 25</p> |
|---|--|

24. Body olive green with brown streak from nostril to orbit; red streak through eye
..... *Hyla cruentomma* (p. 139)
- Body yellowish tan with black flecks; sides and belly silvery gold; no red streak through eye
..... *Hyla rubra* (p. 163)
25. Tan with dark brown lateral stripe from snout through eye to tip of tail
..... *Hyla rossalleni* (p. 162)
- Body pale green above, white below; tail pale orange with brown flecks
..... *Hyla funerea* (p. 143)
26. Dorsal and ventral fins shallow, not more than one-half depth of caudal musculature at midlength of tail 27
- Dorsal and ventral fins more than one-half depth of caudal musculature at midlength of tail 30
27. Upper beak deeply notched; body black with white flecks
..... *Colostethus sauli* (p. 123)
- Upper beak not deeply notched; body brown 28
28. First upper row of denticles on upper lip
..... *Colostethus marchesianus* (p. 121)
- First upper row of denticles inside upper lip 29
29. Body dark brown; tail tan with brown flecks
..... *Dendrobates parvulus* (p. 124)
- Body brown with yellowish tan flecks; tail translucent with brown flecks
..... *Phyllobates femoralis* (p. 126)
30. Lower lip bare 31
24. Cuerpo verde-oliva con línea marrón desde el nostrilo a la órbita; línea roja a través del ojo
..... *Hyla cruentomma* (p. 139)
- Cuerpo marrón-amarillento con pecas negras; costados y vientre oroplateados; sin línea roja a través del ojo
..... *Hyla rubra* (p. 163)
25. Cuerpo marrón claro con banda lateral marrón oscura desde el hocico pasando por el ojo hasta el extremo de la cola *Hyla rossalleni* (p. 162)
- Cuerpo verde-pálido arriba, blanco abajo; cola anaranjada pálida con pecas marrones
..... *Hyla funerea* (p. 143)
26. Aletas dorsales y ventrales bajas, no más altas que media musculatura caudal en la mitad de la cola 27
- Aletas dorsales y ventrales más altas que media musculatura caudal en la mitad de la cola 30
27. Pico superior profundamente escotado; cuerpo negro con pintas blancas *Colostethus sauli* (p. 123)
- Pico superior no profundamente escotado; cuerpo marrón 28
28. Primera fila superior de denticúlos sobre el labio superior
..... *Colostethus marchesianus* (p. 121)
- Primera fila superior de denticúlos por dentro del labio superior 29
29. Cuerpo marrón oscuro; cola marrón clara con pintas marrones
..... *Dendrobates parvulus* (p. 124)
- Cuerpo marrón con pecas marrón-amarillentas; cola traslúcida con pintas marrones
..... *Phyllobates femoralis* (p. 126)
30. Labio inferior desnudo 31

- | | |
|--|--|
| Lower lip bearing papillae 33 | Labio inferior con papilas 33 |
| 31. Beaks robust; body and tail black
..... <i>Bufo marinus</i> (p. 117) | 31. Picos robustos; cuerpo y cola negras
..... <i>Bufo marinus</i> (p. 117) |
| Beaks slender, body and tail brown
..... 32 | Picos débiles; cuerpo y cola marrones
..... 32 |
| 32. Body and tail uniformly dull dark brown <i>Bufo typhoniuss</i> (p. 118) | 32. Cuerpo y cola uniformemente de color marrón-oscuro apagado
..... <i>Bufo typhoniuss</i> (p. 118) |
| Body and tail brown with black flecks on tail
<i>Dendrophryniscus minutus</i> (p. 120) | Cuerpo y cola marrones con pintas negras sobre la cola
<i>Dendrophryniscus minutus</i> (p. 120) |
| 33. Dorsal fin equal to or deeper than caudal musculature and deeper than ventral fin at midlength of tail 34 | 33. Aleta dorsal igual o más alta que la musculatura caudal y más alto que la aleta ventral a mitad de la cola 34 |
| Not so 36 | Diferente 36 |
| 34. Dorsal fin deeper than caudal musculature; body dark green with black flecks; tail olive green
..... <i>Hyla punctata</i> (p. 158) | 34. Aleta dorsal más alta que la musculatura caudal; cuerpo verde oscuro con pecas negras; cola verde-oliva
..... <i>Hyla punctata</i> (p. 158) |
| Dorsal fin equal in depth to caudal musculature; body brown; tail tan with vertical brown markings 35 | Aleta dorsal igual en altura a la musculatura caudal; cuerpo marrón; cola marrón clara con marcas verticales marrones 35 |
| 35. Body dark brown with tan mottling and tan interorbital bar
..... <i>Hyla calcarata</i> (p. 137) | 35. Cuerpo marrón oscuro con motas más claras y con barra interorbital marrón clara
..... <i>Hyla calcarata</i> (p. 137) |
| Body brown above and laterally; venter gray with green lichenous spots <i>Hyla lanciformis</i> (p. 150) | Cuerpo marrón encima y lateralmente; vientre gris con manchas verde-liquenosas
..... <i>Hyla lanciformis</i> (p. 150) |
| 36. Lips not folded laterally 37 | 36. Labios no plegados lateralmente ..
..... 37 |
| Lips folded laterally 38 | Labios plegados lateralmente 38 |
| 37. Body grayish brown with brown interorbital bar; tail brown with orange tint on edge of dorsal fin
<i>Leptodactylus pentadactylus</i>
..... (p. 108) | 37. Cuerpo marrón-grisáceo con barra interorbital marrón; cola marrón con tinte anaranjado sobre el borde de la aleta dorsal
<i>Leptodactylus pentadactylus</i>
..... (p. 108) |

- Body and tail brownish gray with dark flecks on tail
Leptodactylus rhodomystax (p. 111)
38. Two rows of papillae on lower lip
 *Leptodactylus wagneri* (p. 112)
 One row of papillae on lower lip 39
39. Depth of fins greater than musculature *Physalaemus petersi* (p. 115)
 Depth of fins less than musculature 40
40. Body olive-tan; belly gray with gold flecks anteriorly; tail olive-tan with green and orange flecks
 *Leptodactylus mystaceus* (p. 107)
 Body brown with white flecks below; tail brown
Leptodactylus discodactylus
 (p. 105)
41. Body and tail black
 *Hyla geographica* (p. 146)
 Body and tail not black 42
42. One row of labial papillae laterally; dorsum reddish tan with olive-brown markings; belly golden white; tail cream with reddish brown reticulations *Hyla boans* (p. 131)
 Two rows of labial papillae laterally; dorsum greenish brown mottled with dark brown; belly cream with gray spots; tail orange-tan
 *Rana palmipes* (p. 186)
43. One upper row of denticles 44
 No upper rows of denticles 45
- Cuerpo y cola gris-amarronados con pecas oscuras sobre la cola
Leptodactylus rhodomystax (p. 111)
38. Dos corridas de papilas sobre el labio inferior
 *Leptodactylus wagneri* (p. 112)
 Una corrida de papilas sobre el labio inferior 39
39. Altura de las aletas mayor que la de la musculatura *Physalaemus petersi* (p. 115)
 Altura de las aletas menor que la de la musculatura 40
40. Cuerpo marrón-oliváceo; vientre gris con pecas oro anteriormente; cola marrón-oliváceo con pecas anaranjadas
 *Leptodactylus mystaceus* (p. 107)
 Cuerpo marrón con pintas blancas por debajo; cola marrón
Leptodactylus discodactylus
 (p. 105)
41. Cuerpo y cola negras
 *Hyla geographica* (p. 146)
 Cuerpo y cola no negras 42
42. Una corrida de papilas labiales lateralmente; dorso marrón-rojizo con marcas marrón-olivas; vientre blanco-amarillento; cola crema con reticulaciones café-rojizas
 *Hyla boans* (p. 131)
 Dos corridas de papilas labiales lateralmente; dorso marrón-verdoso moteado con marrón oscuro; vientre crema con manchas grises; cola marrón-anaranjada
 *Rana palmipes* (p. 186)
43. Una fila superior de denticulos 44
 Sin filas superiores de denticulos 45

44. Mouth anteroventral; lips folded laterally; body and tail dull pale green *Hyla granosa* (p. 148)

Mouth ventral; lips not folded laterally; unpigmented
..... *Centrolenella midas* (p. 183)

45. Mouth ventral; one row of labial papillae; except for few flecks on caudal musculature, unpigmented
..... *Centrolenella munozorum* (p. 184)

Mouth anteroventral; two rows of labial papillae; body brown; tail cream with brown flecks
..... *Hyla minuta* (p. 155)

44. Boca anteroventral; labios pledagos lateralmente; cuerpo y cola verde-pálidos apagados
..... *Hyla granosa* (p. 148)

Boca ventral; labios no pledagos lateralmente; sin pigmentos
..... *Centrolenella midas* (p. 183)

45. Boca ventral; una corrida de papilas labiales; excepto por algunas pecas en la musculatura caudal, sin pigmentación
..... *Centrolenella munozorum* (p. 184)

Boca anteroventral; dos corridas de papilas labiales; cuerpo marrón; cola crema con pecas marrones
..... *Hyla minuta* (p. 155)

SPECIES ACCOUNTS

The following accounts are arranged systematically by orders and families, and alphabetically by genera and species within families. In the accounts of the snakes, lizards, and amphisbaenians the usage of the name is the same as that in the "Catalogue of the Neotropical Squamata" (Peters and Orejas-Miranda, 1970; Peters and Donoso-Barros, 1970), except where noted in a synonymy. In the synonymies in the accounts of the amphibians, turtles, and crocodilians, the citation to the original description, including the type locality, is given first. Subsequent citations, if any, are to the authority for the present nomenclatural usage or to the most recent taxonomic treatment. The organization of the accounts is by the following side-headings.

Material.—Localities are listed alphabetically with the number of specimens examined from each. In the accounts of the frogs, the number preceding the plus sign indicates frogs, and the number following the sign indicates lots of tadpoles.

Identification.—In most accounts this section is divided into two paragraphs. The first is a diagnosis distinguishing the

species from others in the area. The second includes a description of the species; unless otherwise stated, all colors refer to those of living animals. References to plates are to colored illustrations grouped after page 192. The measurements given at the end of the section are the maximum sizes for males and females in the study area. These measurements are snout-vent length (frogs), snout-vent length + tail length (salamanders, crocodilians, lizards, and snakes), total length (caecilians), and carapace length (turtles).

Occurrence.—The data on seasonal and diel activity, habitat, and behavior are summarized in this section.

Life History.—Information on reproductive cycles, fecundity, breeding sites and behavior, oviposition sites, duration of development, and emergence of young are presented in this section.

Tadpoles.—In accounts of frogs, where applicable, descriptions of tadpoles and their habitat and behavior are given. Developmental stages of tadpoles are those of Gosner (1960).

Mating Call.—In accounts of frogs,

the mating call is described in this section; terminology follows Duellman (1970b).

Food.—The food habits of the species are summarized in this section (not included in accounts of caecilians, crocodilians, and turtles).

Taxonomic Comments.—Where appropriate, discussion of variation, taxonomic status, and nomenclature, are presented.

Remarks.—Any additional information not referable to any other sections is included in this category.

Throughout the species accounts, the following abbreviations will be used: *sec* = second; *min* = minute; and *Hz* = Hertz.

CAECILIANS

CAECILIIDAE

Caecilia disossea Taylor

Caecilia disossea Taylor, 1968, Caecilians World:374 [Type locality.—Río Santiago, Perú].

Material.—Lago Agrio, 2; Santa Cecilia, 4.

Identification.—This is one of two caecilians in the area that are extremely elongate, having a body length more than 80 times the diameter. In *Caecilia disossea* the eye is in a bony socket and is not covered by bone. In the other species, *Osaecilia bassleri*, the eye is covered by a thin layer of bone. The other caecilians in the area are more robust. The entire animal is black with minute blue flecks, giving it a gray appearance; the edge of the lower lip is pale gray. ♂ 1170 mm; ♀ 661 mm.

Occurrence.—Two were moving in a clearing after heavy rains; one was unearthed from a stream-bank in a clearing, and two were uncovered by bulldozers in clearing primary forest.

Life History.—The two females, both from June, contained small ova.

Caecilia tentaculata Linnaeus

Caecilia tentaculata Linnaeus, 1758, *Systema Naturae*, Ed. 10:229 [Type locality.—Suri-nam].

Material.—Lago Agrio, 11; Santa Cecilia, 17.

Identification.—This large, heavy-bodied caecilian has a body length about 30-35 times the diameter of the body. In this respect it differs from the slender caecilians (*Caecilia disossea* and *Osaecilia bassleri*) that have a length more than 80 times the diameter. *Caecilia tentaculata* is dark bluish gray above, slightly paler below, and lacks any pale markings. Other heavy bodied caecilians in the area have pale markings – head in *Microcaecilia albiceps* and narrow rings on body in *Siphonops annulatus*. The eye of *C. tentaculata* usually is evident as a dark spot below the skin. ♂ 901 mm; ♀ 987 mm.

Occurrence.—One was in a wet grassy clearing by day; three were removed from a trench in secondary forest. One was under a log in primary forest, and most of the others were unearthed by bulldozers during the clearing of primary forest.

Life History.—Five adult females are in the collection; three from May show no evidence of reproductive activity, whereas two from July have small ova.

Microcaecilia albiceps (Boulenger)

Dermophis albiceps Boulenger, 1882, Cat. Batr. Grad. Caud. Batr. Apoda Brit. Mus.:98 [Type locality.—Ecuador].

Microcaecilia albiceps—Taylor, 1968, Caecilians World:532.

Material.—Lago Agrio, 24; Santa Cecilia, 1.

Identification.—This small caecilian is dark bluish gray with a creamy white to pale pink head. In some individuals the tip of the tail is pale gray. No other caecilian in the area has a contrastingly colored head. The length of the body is 40-48 times the diameter. ♂ 235 mm; ♀ 206 mm.

Occurrence.—One individual was found under a log in primary forest at Santa Cecilia; the large series from Lago Agrio was obtained by following bulldozers clearing primary forest.

Life History.—Seven of nine females collected from 29 April to 24 May contained small ova; the other two showed no evidence of reproductive activity.

Oscaecilia bassleri (Dunn)

Caecilia bassleri Dunn, 1942, Bull. Mus. Comp. Zool., 91:518 [Type locality.—Río Pastaza, Ecuador].

Oscaccilia bassleri—Taylor, 1968, *Caecilians* World:600.

Material.—Lago Agrio, 5.

Identification.—This long, slender caecilian can be confused with *Caecilia disossea*; the length of the body is 90-140 times the diameter in *O. bassleri*. All other caecilians, except *C. disossea*, have much heavier bodies. In *Oscaecilia* the eye is visible under a thin layer of bone, whereas in *Caecilia disossea* the eye is in a socket and not covered by bone. The animal is uniform dull bluish black dorsally and slightly paler below. ♂ 864 mm; ♀ 774 mm.

Occurrence.—All were obtained during clearing of primary forest by bulldozers.

Life History.—One of two females obtained in May contained small ova.

Siphonops annulatus (Mikan)

Caecilia annuata Mikan, 1820, *Delectus Floriae Fauna Brasil*, pl. 11 [Type locality.—"Sebastianopolis" (=Rio de Janeiro), Brasil].
Siphonops annulatus—Wagler, 1830, *Isis von Oken*, 21:742.

Material.—Puerto Libre, 1.

Identification.—This is a stout-bodied caecilian with a body length 32 times the diameter. The head and body are dark bluish black with narrow pale bluish white rings corresponding to the primary folds on the body. No other caecilian in the area is so colored. ♂ 454 mm.

Occurrence.—The specimen was in a

trench in early morning; presumably it fell in during the night.

Life History.—No data are available.

SALAMANDERS

PLETHODONTIDAE

Bolitoglossa equatoriana

Brame and Wake

Bolitoglossa equatoriana Brame and Wake, 1971, Contr. Sci. Los Angeles Co. Mus., 219:23 [Type locality.—Limoncocha, Provincia Napo, Ecuador].

Material.—Santa Cecilia, 3.

Identification.—This is the largest salamander in the area. By comparison with *B. peruviana*, this species is not only larger but proportionately more robust. Furthermore, the venter in *B. equatoriana* is dark with large white spots, whereas the venter in *B. peruviana* is gray with small pale flecks. In *B. equatoriana* the dorsum is reddish brown; the proximal parts of the hind limbs are dull yellow. The venter is gray with white flecks clumped into irregular spots. The iris is bronze. ♂ 44+44 mm, ♀ 52+47 mm.

Occurrence.—The three individuals were found at night on low vegetation in secondary forest. One is from August and two from September.

Life History.—The single female obtained in September had small ovarian eggs.

Food.—All specimens contained ants; two also contained small beetles, and one had a small wasp.

Remarks.—Our specimens conform to the description given by Brame and Wake (1971). Formerly the species was known only from Limoncocha, about 65 km SE of Santa Cecilia.

Bolitoglossa peruviana (Boulenger)

(FIGURE 48)

Spelerpes peruviana Boulenger, 1883, Ann. Mag. Nat. Hist., (5)12:165 [Type locality.—Moyobamba, Departamento San Martín, Perú].
Bolitoglossa peruviana—Taylor, 1944, Univ. Kansas Sci. Bull., 30:219.



FIG. 48.—*Bolitoglossa peruviana*. Upper: juvenile, 22 mm SVL (KU 124125); lower: juvenile, 24 mm SVL (KU 124126).

Material.—Puerto Libre, 100; Santa Cecilia, 19.

Identification.—This small, relatively slender salamander differs from the larger, more robust *B. equatoriana* by having scattered small pale flecks, instead of flecks clumped into spots, on the venter. In *B. peruviana* the dorsum is tan, with or without a median brown streak at night; by day the dorsum is reddish brown or dull tan with dark brown streaks or flecks and (in some individuals) a brown triangle on the head. The venter is gray with scattered silvery white to gold flecks. The iris is tan with an orange ring around the pupil. ♂ 32+27 mm, ♀ 43+38 mm.

Occurrence.—All of the specimens from Puerto Libre were collected in July. Three specimens were obtained by day; two were in leaf litter in primary forest, and one was under a fallen palm frond in secondary forest. The others were found at night in secondary forest. Most of the salamanders were on leaves of low plants, principally ferns between 5 and 30 cm above the ground, but a few were found as high as 1 m above the ground, and two were at heights of more than 1.5 m. Five were in primary forest, one on a banana plant, and the rest in secondary forest.

Life History.—Thirty-eight females contained 6-13 ($\bar{x}=8.39$) ovarian eggs; 32 of these females were obtained in July at Puerto Libre. The other six are from Santa Cecilia; one was obtained in each month (April–September). Of 20 additional females taken in July at Puerto Libre, seven contained immature ovarian eggs, and 13 showed no evidence of reproductive activity. At Santa Cecilia juveniles (< 25 mm SVL) were found in June, July, and February; no salamanders were found in October–January. The presence of juveniles from different times of the year and of gravid females from every month in which females were found is indicative of a lengthy breeding season or perhaps acyclic breeding in this species—an hypothesis supported by the absence of size classes in the large series obtained at Puerto Libre in July (Fig. 49).

The smallest gravid females have snout-vent lengths of 30 mm and ovarian complements of 6, 8, and 9 eggs. The two largest females have snout-vent lengths of 37 and 39 mm; each has an ovarian complement of 10 eggs. The largest ovarian complement, 13, is in a female having a snout-vent length of 33 mm. In the series of 38 gravid females, only a slight positive correlation $r=0.19$) exists between ovarian complement and snout-vent length.

Food.—The stomachs of 14 adults contained primarily ants, accounting for 172 of 190 prey items. Other prey included 13 beetle larvae, 1 beetle, 2 spiders, 1 mite, and 1 leafhopper (Cicadellidae).

Taxonomic Comments.—Two small species of *Bolitoglossa* are known from the Amazon Basin — *B. peruviana* Boulenger and *B. altamazonica* Cope. Identifications of series of specimens obtained in Ecuador and Brasil have been confirmed by David B. Wake. A series of *B. altamazonica* from the vicinity of Belém, Brasil, was compared with the series of *B. peruviana* from Puerto Libre, by Mar-

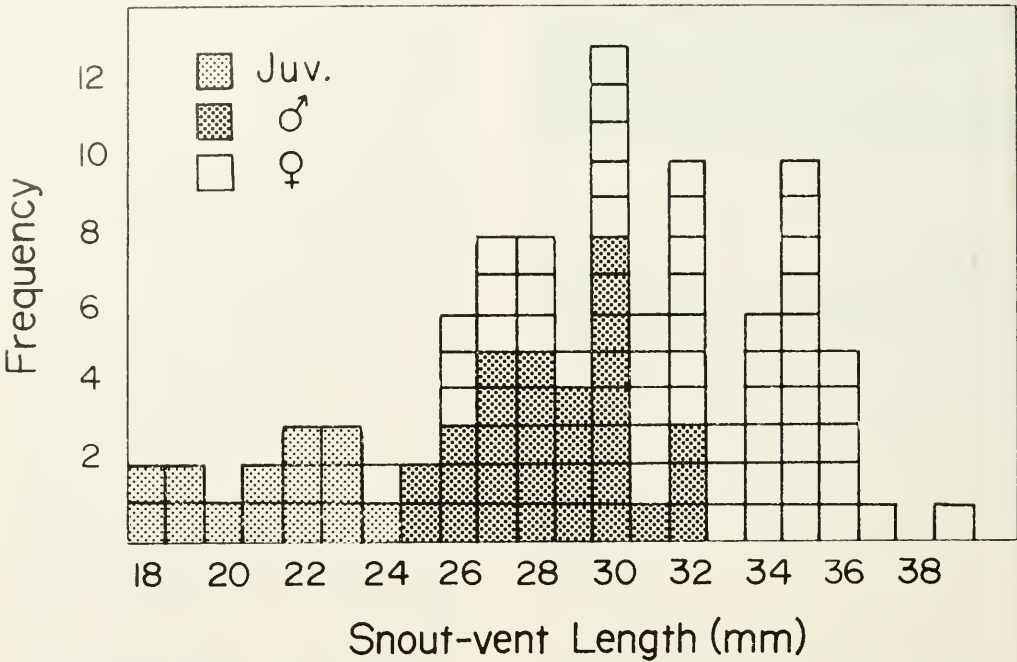


FIG. 49.—Frequency distribution of snout-vent lengths of 100 *Bolitoglossa peruviana* collected in July 1968 at Puerto Libre, Ecuador.

tha L. Crump, who generously provided the results of her analysis (Table 4). Although average differences are noted in several morphometric characters, the principal structural differences between the samples are that *B. peruviana* is smaller with a proportionately shorter tail, larger eye, and fewer maxillary and vomerine teeth.

Although the coloration of the two species is similar, *B. altamazonica* is more variable. The dorsal ground color is dark gray to reddish brown, and the venter is gray, flecked with white in many individuals. In some specimens the dorsum is unicolor, whereas in others the dorsum is mottled or has a middorsal stripe, lighter or darker than the ground color. All individuals have a dark brown triangular mark with the base between the eyes and the apex posteriorly. Some individuals have white flecks on the limbs, flanks, and lateral surfaces of the tail.

Brame and Wake (1971) recognized *B. altamazonica* and *B. peruviana* as the

only members of an Amazonian species group of *Bolitoglossa*. The former is known from Colombia, Perú, Bolivia, and extreme western Brasil in the upper Amazon Basin and from the vicinity of Belém, Brasil, near the mouth of the Amazon. *Bolitoglossa peruviana* is known from one locality in Perú and three in Ecuador. The two species have not been found at the same locality (see Brame and Wake, 1963, for distribution map).

FROGS

PIPIDAE

Pipa pipa (Linnaeus)

Rana pipa Linnaeus, 1758, Syst. Nat., Stockholm, Ed. 10, 1:210 [Type locality.—Suri-nam].

Pipa pipa—Barbour, 1923, Proc. New England Zool. Club, 9:3.

Material.—Santa Cecilia, 8.

Identification.—This aquatic frog cannot be confused with any other from the area. The body is depressed, and the

TABLE 4.—Comparison of Morphometric and Dentitional Characters in *Bolitoglossa altamazonica* and *B. peruviana*
(The range is followed by the mean ± 1 standard error; significance levels of *t*-test are between sexes.)

Character	<i>B. altamazonica</i> 9 ♂♂	<i>B. altamazonica</i> 7 ♀♀	<i>B. peruviana</i> 15 ♂♂	<i>B. peruviana</i> 41 ♀♀	<i>P</i>
Snout-vent Length	31.7-40.1 (36.1 $\pm$ 0.9)	37.4-49.2 (43.5 $\pm$ 1.4)	27.3-31.9 (29.2 $\pm$ 0.3)	30.1-42.3 (33.8 $\pm$ 0.4)	<.001
Tail Length	25.1-41.5 (32.8 $\pm$ 1.6)	35.0-40.0 (36.7 $\pm$ 0.9)	19.0-27.0 (24.0 $\pm$ 0.5)	20.2-37.6 (25.5 $\pm$ 0.5)	-----
Head Width	4.6-6.0 (5.5 $\pm$ 0.1)	5.8-7.2 (6.3 $\pm$ 0.2)	4.7-5.7 (5.1 $\pm$ 0.1)	5.0-6.1 (5.4 $\pm$ 0.04)	<.001
Diameter of Eye	1.8-2.4 (2.0 $\pm$ 0.1)	2.0-2.3 (2.2 $\pm$ 0.04)	1.5-2.7 (1.9 $\pm$ 0.1)	1.5-2.5 (2.0 $\pm$ 0.03)	-----
Width Forefoot	2.2-3.2 (2.7 $\pm$ 0.1)	2.7-3.3 (3.0 $\pm$ 0.1)	1.7-2.7 (2.2 $\pm$ 0.1)	2.0-3.3 (2.5 $\pm$ 0.04)	<.001
Width Hind Foot	2.9-4.0 (3.5 $\pm$ 0.1)	3.5-4.2 (3.9 $\pm$ 0.1)	2.7-3.3 (3.0 $\pm$ 0.05)	2.6-4.1 (3.2 $\pm$ 0.05)	<.001
Maxillary Teeth	12-33 (19.7 $\pm$ 2.0)	23-33 (27.4 $\pm$ 1.5)	10-25 (17.6 $\pm$ 1.2)	12-48 (23.6 $\pm$ 1.1)	<.001
Vomerine Teeth	11-18 (14.0 $\pm$ 0.7)	12-24 (16.7 $\pm$ 1.6)	9-23 (14.6 $\pm$ 0.9)	6-33 (16.4 $\pm$ 0.8)	-----

head is broad, flattened, and triangular with a truncate snout and dermal folds at the corners of the large mouth. The eyes are minute and dorsal in position. The toes are fully webbed; the long, unwebbed fingers terminate in star-shaped structures. The dorsum is dull brown with, or without, small scattered darker brown spots; the venter is dull tan with creamy flecks and blotches. The skin on the dorsum is finely tuberculate. All specimens from Santa Cecilia are juveniles; the largest has a snout-vent length of 78 mm. Adults in excess of 150 mm snout-vent length are known from other localities.

Occurrence.—*Pipa pipa* was found only in permanent ponds in the forest.

Life History.—No observations were made on this species; eggs are carried on the back of the female and develop directly into small frogs (Rabb and Snedigar, 1960; Rabb and Rabb, 1960, 1963).

Mating Call.—The call is a series of clicks produced underwater by movement of the arytenoid bones within a bony laryngeal structure formed by hyoid elements (Rabb, 1960).

Food.—A specimen 78 mm in length contained two fish — an *Erythrinus erythrinus* (Erythrinidae) 30 mm long and a somewhat smaller pimelodid catfish.

Remarks.—Apparently this is the first report of the genus from Ecuador. Dunn (1948:11) noted its widespread occurrence in the Amazon Basin and the absence of records from Ecuador.

LEPTODACTYLIDAE

Adenomera andreae (Müller)

(FIGURE 50)

Adenomera andreae Müller, 1923, Zool. Anz., Leipzig, 57:40 [Type locality.—Peixeboi, Estado do Pará, Brasil]. Heyer, 1973, Contr. Sci. Los Angeles Co. Mus., 251:29.

Adenomera andreae—Heyer, 1974, Contr. Sci. Nat. Hist. Mus. Los Angeles Co., 253:4.

Material.—Lago Agrio, 3; Puerto Libre, 32; Santa Cecilia, 43.



FIG. 50.—*Adenomera andreae*, ♀, 26 mm SVL (KU 119323).

Identification.—This small species differs from *Leptodactylus* in the area by having the first and second fingers equal in length. It is most easily confused with small individuals of *Leptodactylus discodactylus* and *L. wagneri*, both of which have the first finger longer than the second and have lateral fringes on the toes. Other species of *Leptodactylus* in the area have dorsolateral dermal folds, which are absent in *Adenomera* and in *L. discodactylus* and *wagneri*. However, elongate tubercular ridges are present laterally in *Adenomera*; in most individuals a prominent ridge extends diagonally from the scapular region to the groin. The absence of expanded tips on the digits distinguishes *Adenomera* from most *Eleutherodactylus*, and the absence of webbing distinguishes it from *Rana*. *Adenomera andreae* superficially resembles *Eleutherodactylus nigrovittatus*, which has smooth skin dorsally, has a dark anal patch, and lacks an interorbital triangular mark.

The dorsum is dull olive-brown to grayish brown with darker brown markings consisting of an interorbital triangle with apex posteriorly; short, broad longitudinal bars behind tympanum, in groin, and posteriorly from scapular region; diagonal bar in groin; round spots on flanks; and transverse bars on hind limbs. The upper lip is marked by two dark brown suborbital bars diverging from the

eye. A short creamy white bar extends from the tympanum to the base of the arm, which is orange-tan. The posterior surfaces of the thighs are brown. The venter is creamy white with brown flecks peripherally on the chin and laterally on the belly and thighs in some individuals. The iris is dull bronze with black reticulations. Nuptial pads and spines are absent in breeding males. ♂ 25 mm; ♀ 27 mm.

Occurrence.—This small terrestrial frog is active by night and day throughout the year, although about 60 percent of the frogs were found at night. Ten individuals were hidden beneath logs by day, and two were resting on low vegetation at night. Eighty percent of the frogs were in leaf litter in primary or secondary forest; only one individual was in water. Eleven individuals were found in clearings at night.

Life History.—No males were heard calling. Females having mature ovarian eggs were found in February, March, May, July, August, and September; females having immature ovarian eggs were found in February-May and July-October. Five or more females were found in each of three months; the percentage of females having mature ovarian eggs in each of those months is May (62%, $N=8$), July (70%, $N=20$), August (40%, $N=5$). The data are insufficient to determine with certainty the seasonal nature of reproduction in this species.

The species of *Adenomera* deposit terrestrial foam nests, in which the larvae complete their development (Heyer, 1973). A foam nest, presumably, produced by *A. andreae*, was found beneath a log in primary forest in March 1967. Twelve females contained 6-16 ($\bar{x}=8.7$) unpigmented eggs having a maximum diameter of 3.0 mm. Of the three smallest juveniles (snout-vent lengths of 13-14 mm), one is from June and two from July.

Mating Call.—The call is unknown.

Food.—Of 11 specimens containing food, ants were present in five. Roaches

(Blattidae) and beetles were present in two stomachs, whereas each of the following food items was present in only one individual: Dermaptera, Isoptera, Hemiptera, Homoptera, Chilopoda, Araneae, and Annelida.

Taxonomic Comments.—Most of the specimens from the Santa Cecilia region were utilized by Heyer (1973) in his systematic analysis of the *Leptodactylus marmoratus* group. Heyer resurrected the name *L. andreae* for an Amazonian species which had been confused with *L. hylaedactylus*; Heyer (1974a) resurrected the generic name *Adenomera* Fitzinger for members of the *Leptodactylus marmoratus* group.

***Ceratophrys cornuta* (Linnaeus)**

(FIGURE 51)

Rana cornuta Linnaeus, 1758, Syst. Nat., Stockholm, Ed. 10, 1:212 [Type locality.—“Virginia”].

Ceratophrys cornuta—Peters, Monatsb. Akad. Wiss. Berlin, 1872:204.

Material.—Santa Cecilia, 1+1.

Identification.—This large distinctive frog has a broad head (> 50% of snout-vent length) and dermal “horns” on the eyelids. The only other frog in the area with large dermal “horns” on the eyelids is *Hemiphractus proboscideus*, which has a fleshy proboscis and a depressed body, in marked contrast to the robust body of *Ceratophrys*.

The dorsum is brown and tan. A broad middorsal tan stripe begins on the eyelids, narrows in the occipital region, and extends to the vent. The stripe is bordered by dark brown; dorsolaterally there is a complex design of brown and tan. The side of the head is grayish tan with diagonal brown marks. The limbs are brown with dark brown transverse bars. The posterior surfaces of the thighs are brown with indistinct yellow mottling. The posterior part of the flanks, anterior surfaces of thighs, and inner surfaces of shanks are brown mottled with yellow. The belly is mottled brown and gray. The throat and ventral sur-



FIG. 51.—*Ceratophrys cornuta*, ♂, 80 mm SVL (UMMZ 129287).

faces of the hands and feet are dark brown. The iris is creamy bronze with a median horizontal red streak. The single specimen from Santa Cecilia (UMMZ 129287) is a male having a snout-vent length of 80 mm, but Ronn Altig has a living male from Santa Cecilia with a snout-vent length of 110 mm.

Occurrence.—The single specimen was sitting on the ground in secondary forest on the night of 15 May 1969.

Life History.—No data are available other than the presence of tadpoles in a pond in May.

Tadpoles.—The following description is based on a tadpole (KU 158500) in stage 35 having a body length of 19 mm and a total length of 56 mm. The body is elongately ovoid, wider than deep, and widest just anterior to the eyes. The snout is round. The eyes are small, close together, and directed anterolaterally. The nostrils are directed laterally at a point about one-third of the distance between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterolaterally on the ventrolateral surface of the body at about midlength of the body. The cloacal tube is short and dextral. The caudal musculature is moderately robust proximally and gradually tapers to a slender tip. The fins are equal in depth and deepest at the midlength of the tail, where each fin is slightly deeper than the caudal musculature. The fins extend to the tip of the

pointed tail, and the dorsal fin does not extend onto the body. The tail comprises about 66 percent of the total length. The large mouth is anterior with expanded protruding lips, each bearing a single row of large pointed papillae. The beaks are massive; the lower beak has a medial spine that fits into a notch in the upper beak. There are nine upper and nine lower rows of denticles, plus some short rows lateral to the beaks. The three innermost rows of both series are interrupted medially. The body is dull brown; the tail is tan with a brown stripe laterally on the proximal one-third of the tail. The entire caudal musculature and dorsal fin bear fine brown reticulations; the ventral fin is unpigmented.

Mating Call.—The call is unknown.

Food.—The specimen contained an adult frog, *Edalorhina perezii*, one spider, and four orthopterans.

Edalorhina perezii Jiménez de la Espada

(PLATE 1)

Edalorhina perezii Jiménez de la Espada, 1871, J. Sci. Acad. Lisboa, 3:58 [Type locality.—banks of the Río Napo, Ecuador].

Material.—Lago Agrio, 3; Santa Cecilia, 5.

Identification.—This frog with a depressed body, cluster of tubercles on the eyelids, tubercle on snout, dorsolateral dermal fold, and black and white belly is distinct from all other frogs in the area. *Eleutherodactylus orphnolaimus* has tubercles on the eyelid but lacks dorsolateral dermal folds; *Ceratophrys cornuta* and *Hemiphractus proboscideus* have single dermal "horns" on the eyelids but differ in structure and coloration. *Edalorhina perezii* is unique in having a white venter with large black spots laterally.

The skin on the dorsum bears 5-7 longitudinal tubercular folds or two or three transverse folds; diagonal tubercular folds are present on the dorsal surfaces of the limbs. The dorsum is brown with tan streaks, or tan with a pale green suffusion on the snout, eyelids, flanks,

knees, and heels. There is a dark brown interorbital bar and transverse bars on the limbs. The flanks and ventrolateral surfaces are black. A yellow-orange spot is present in the groin. The anterior and posterior surfaces of the thighs, ventral surfaces of shanks, and inner surfaces of the feet are black and yellow or orange. The throat and belly are white, except for large black areas laterally on the belly. The iris is bronze with radiating gray-brown bars. ♂ 33 mm; ♀ 36 mm.

Occurrence.—All were found active by day amidst leaf litter on the ground in primary forest. The frogs moved by series of short hops and hid amongst dead leaves, where they were effectively camouflaged.

Life History.—One female collected in May contained 69 ovarian eggs, a second showed no evidence of reproductive activity. Three juveniles from April and May have snout-vent lengths of 16 and 17 mm. No tadpoles were found, nor was any breeding activity observed.

Mating Call.—The call is unknown.

Food.—Four individuals contained food—Diptera (2), Hymenoptera (1), Orthoptera (1).

Taxonomic Comments.—Dunn (1949) noted the variation in the presence or absence of prevomerine teeth and polymorphism in dorsal tubercular folds (longitudinal or transverse). Of six adults, one has longitudinal folds and no teeth; two have longitudinal folds and teeth, and three have transverse folds and no teeth. The only specimens having streaked brown and tan dorsal surfaces are those having longitudinal folds. In other aspects of coloration, the morphs are identical.

Eleutherodactylus acuminatus Shreve

(FIGURE 52)

Eleutherodactylus acuminatus Shreve, 1935. Occas. Papers, Boston Soc. Nat. Hist., 8: 217 [Type locality.—Canclos, Provincia Pastaza, Ecuador].

Material.—Lago Agrio, 3; Puerto Libre, 6; Santa Cecilia, 26.

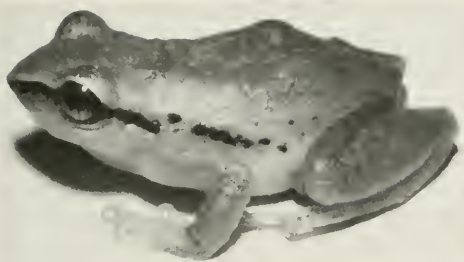


FIG. 52.—*Eleutherodactylus acuminatus*, ♀, 31 mm SVL (KU 148720).

Identification.—This is one of three species of green *Eleutherodactylus* in the area; the others are *E. pseudoacuminatus* and *paululus*, both of which are smaller species having an external tympanum. The tympanum is not visible in *E. acuminatus*, which has a black stripe from the snout through the eye and extending to a point above the arm. The only other species of *Eleutherodactylus* in the area lacking an external tympanum are *E. croceoinguinis*, *martiae*, and *E. quaquaversus*, which are predominantly brown frogs lacking a black canthal stripe. Other small green frogs in the area are three species of *Centrolenella*, two species of *Sphaenorhynchus*, *Hyla granosa* and *H. punctata*; all of these have tympana and extensive webbing between the toes. Webbing is absent in *E. acuminatus*.

The snout is pointed and projects beyond the margin of the lip. The skin is smooth on the dorsum and granular on the belly; dorsal tubercles and folds are absent. The discs on the fingers are broadly expanded. The dorsum and the anterior and posterior surfaces of the thighs are pale green; the venter and flanks are white, and the throat is greenish yellow. In some individuals a few small black spots are present dorsolaterally on the anterior part of the flanks; these extend posteriorly from the end of the black stripe extending from the tip of the snout, through the eye, to a point above the axilla. The iris is pale bronze. ♂ 21 mm; ♀ 31 mm.

Occurrence.—With the exception of one individual found amidst leaf litter on the forest floor by day and one on the ground in a clearing at night, all individuals were found in bushes and trees. Seven were in bromeliads by day; all others were sitting on leaves of bushes and trees at night. Most frogs were on leaves of bushes less than 1.5 m above the ground in secondary forest, but three were higher, and six were in primary forest.

Life History.—Although adult females were found in all months except February, March, November, and December, females with mature ovarian eggs were found only in May (3), July (2), and August (1). The six gravid females were 27.0–31.0 ($\bar{X}$ = 28.8) mm in snout-vent length and contained 12–21 ($\bar{X}$ = 17.2) eggs, the largest of which was 2.4 mm in diameter. An amplexant pair was found on a bush on 23 May 1972. Possibly eggs are deposited in bromeliads, where development is direct. The smallest juveniles (14.0–15.0 mm), found in June and July, probably are not recent hatchlings. The data are insufficient to determine the extent of the breeding season in *E. acuminatus*; I suspect that breeding occurs throughout a much longer period than that suggested by the dates of collection of gravid females.

Mating Call.—The mating call is a short, high whistle repeated infrequently.

Food.—Of 24 stomachs examined, 23 contained 165 ants; other food items included two small beetles and one small homopteran.

Eleutherodactylus altamazonicus

Barbour and Dunn

(FIGURE 53)

Eleutherodactylus altamazonicus Barbour and Dunn, 1921, Proc. Biol. Soc. Washington, 34:161 [Type locality.—probably Nauta, Departamento Loreto, Perú].

Material.—Lago Agrio, 21; Puerto Libre, 53; Puerto Ore, 2; Santa Cecilia, 136.

Identification.—This small species of

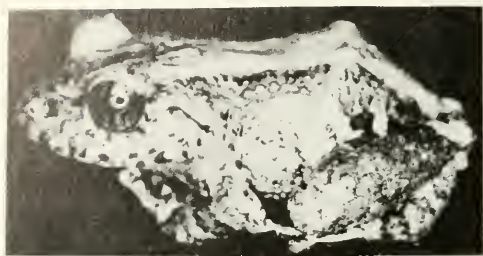


FIG. 53.—*Eleutherodactylus altamazonicus*, ♀, 26 mm SVL (KU 110777).

Eleutherodactylus with a partially concealed tympanum has black and cream, bluish white, or rose pink mottling in the groin and on the posterior surfaces of the thighs. The only other species having similar coloration is the larger *E. diadematus*. The latter has bluish white or pale gray and diagonal black bars in the groin. The two species also can be distinguished by the shape of the snout (pointed tip in *E. altamazonicus* and round in *E. diadematus*), and ventral coloration (brown or gray with white flecks in *E. altamazonicus* and cream with brown reticulations in *E. diadematus*), texture of the skin on the dorsum (tubercular in *E. altamazonicus* and smooth with scattered pustules in *E. diadematus*, which has a prominent tympanum). Other species having pale spots on the posterior surfaces of the thighs either have smooth skin on the venter (*E. conspicillatus* and *E. lathanites*) or short unexpanded digits (*E. sulcatus*). *Eleutherodactylus altamazonicus* superficially resembles another small species with tubercular skin on the dorsum (*E. croceinguinis*), which is readily distinguished by the presence of a large deep yellow to orange spot in the groin.

The snout is nearly truncate in dorsal view except for a projecting tip, which provides a pointed profile. The tips of the fingers are expanded about thrice the width of the digit and are truncate. An exterior tympanum is rarely present. The skin on the dorsum is tubercular, and that on the belly is granular. The dorsum varies from tan to reddish brown.

Many individuals are tan to pale reddish brown dorsally with the side of the head and flanks dark brown. In others the dorsum is brown with a pale tan interorbital bar and W-shaped mark in the scapular region, each bordered posteriorly by a corresponding dark brown mark. The lips are barred; canthal and postorbital stripes are absent. The flanks are dark brown or tan or gray with broad diagonal dark brown marks. The dorsal surfaces of the limbs are brown with dark brown transverse bars; some individuals have pale tan heels. The inguinal region, proximal anterior surfaces of the thighs, and the posterior surfaces of the thighs are mottled or barred with black or dark brown and cream, bluish white, or rose-pink. The ventral surfaces are gray brown to dark brown with minute white flecks. The iris is reddish copper with a gray suffusion. ♂ 22mm; ♀ 34 mm.

Occurrence.—Two individuals were found on the ground at night in clearings, and one was on a banana plant at night. All others were in primary forest (9%) or secondary forest (91%). Of those in the forest, 15 were on the forest floor by day, and 147 were on vegetation at night; two of the latter were on tree trunks, and the others were on leaves less than 1.5 m above the ground.

Life History.—Of 85 adult females, 44 were gravid; these were found throughout the year, except December thru February. Two non-gravid females were found in February. Twenty gravid females had snout-vent lengths of 27.0–31.5 ($\bar{X}$ =28.1) mm and contained 12–25 ($\bar{X}$ =18.2) ovarian eggs, the largest of which had a diameter of 2.5 mm. Amplectant pairs were found on low vegetation at night from May through November; four of the 13 pairs were found in August. Three pairs laid eggs in the laboratory on 25 and 26 August and 24 November 1971. The clutches consisted of 17, 19, and 20 unpigmented eggs having diameters of 3.1, 2.3, and 3.0 mm, respectively. None of the eggs hatched. The four smallest juveniles had snout-

vent lengths of 8.0-10.0 ($\bar{X}$ =9.0) mm and were found in July. Evidently reproduction occurs throughout the year. Presumably the eggs are deposited amidst leaf litter or other debris on the forest floor.

Mating Call.—The mating call is a soft “cluck”, repeated once or twice in succession.

Food.—Twenty-six individuals had eaten a variety of small arthropods, among which orthopterans were the most frequent prey (34.6% of stomachs), followed by ants (26.9%), beetles (15.4%), spiders (15.4%), dipteran larvae (11.5%), and beetle larvae (7.7%).

Eleutherodactylus conspicillatus

(Günther)

(FIGURE 54)

Hylodes conspicillatus Günther, 1859, Cat. Batr. Sal. Brit. Mus., London: 92 [Type locality.—Andes of Ecuador].

Eleutherodactylus conspicillatus—Rivero, 1961, Bull. Mus. Comp. Zool., 126:63.

Material.—Lago Agrio, 2; Puerto Libre, 19; Santa Cecilia, 100.

Identification. — *Eleutherodactylus conspicillatus* is one of three species of *Eleutherodactylus* in the area that has smooth skin on the venter. This species and *E. lanthanites* have dorsolateral dermal folds, and broadly expanded terminal discs on the fingers and toes. *Eleutherodactylus lanthanites* has a gray throat with a median white streak, a pale canthal stripe bordered below by a brown stripe, and pale creamy tan flecks on brown ground color on the posterior surfaces of the thighs, whereas *E. conspicillatus* has a creamy white throat, a distinct narrow creamy white canthal stripe with the side of the head black below the stripe, and bright orange or red flecks on a dark brown ground color on the posterior surfaces of the thighs. The only other species having smooth skin on the venter is *E. nigrovittatus*, which lacks dorsolateral folds and expanded discs. Three other species (*E. altamazonicus*, *diadematus*, and *sulca-*



FIG. 54.—*Eleutherodactylus conspicillatus*, ♂, 27 mm SVL (KU 110784).

tus) have pale spots on the posterior surfaces of the thighs, but in these species the spots are large, and the skin on the belly is granular. In coloration *E. conspicillatus* superficially resembles the much larger *Hyla lanciformis*, which has granular ventral skin and extensive webbing between the toes.

The snout is narrow and rounded and projects slightly beyond the margin of the lip. The skin is finely granular on the dorsum and smooth on the venter; dorsal tubercles are absent, but narrow, low dorsolateral dermal folds are present. The discs on the fingers are expanded and round, about twice the width of the digit. An external tympanum is present.

The dorsum and flanks vary from dull olive-green to pinkish tan with darker olive or brown markings, each usually narrowly outlined with cream. The markings consist of a broad interorbital bar and two or three chevrons on the back; the apex of each chevron is anterior and the lateral ends terminate on the flanks. The dorsal surfaces of the limbs are marked with diagonal dark bars about half as wide as the interspaces. The side of the head is black, and a black postorbital stripe angles ventrally just posterior to the tympanum. The canthal stripe is creamy yellow to white and begins on the tip of the snout. In most individuals the narrow dorsolateral folds are cream. The groin and anterior surfaces of the thighs are pinkish tan to orange; the posterior surfaces of the thighs are dark brown with orange or red flecks. The belly is white, with

or without gray flecks; the ventral surfaces of the limbs are pale gray. The iris is deep bronze with a median horizontal brown streak. ♂ 31 mm; ♀ 44 mm.

Occurrence.—*Eleutherodactylus conspicillatus* is a conspicuous forest inhabitant. Individuals are active on the forest floor by day and on the ground or low vegetation at night. The following analysis is based on data on 107 individuals: 56 in primary forest, 51 in secondary forest; 42 on ground by day, 7 at night, and 58 on vegetation (< 1.5 m) at night. The frogs are active both night and day. During the day they are most active on the ground early in the morning or immediately after showers. At night they perch on leaves or branches; all seemed to be awake at night.

Life History.—Only 12 gravid females were found: April (3), May (2), July (5), August (1), September (1); non-gravid females were found in those months and in February, June, and November. Gravid females had snout-vent lengths of 40.0–44.5 ($\bar{X}$ =42.3) mm and contained 27–62 ($\bar{X}$ =42.8) ovarian eggs. The largest eggs had diameters of 3.5 mm. One juvenile with a snout-vent length of 13.0 mm was found in May, and three (10.0, 12.0 and 13.0 mm) were found in July. Although the data are inconclusive, I suspect that *E. conspicillatus* breeds throughout the year with the possible exception of periodic dry times. Presumably the eggs are deposited amidst leaf litter on the forest floor.

Mating Call.—The call consists of a series of low-pitched soft notes.

Food.—Although several kinds of arthropods were present in 27 stomachs, orthopterans (74% of the stomachs) and spiders (26%) were the most abundant food items.

Eleutherodactylus croceinguinis Lynch

(FIGURE 55)

Eleutherodactylus croceinguinis Lynch, 1968, J. Herp., 2:133 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

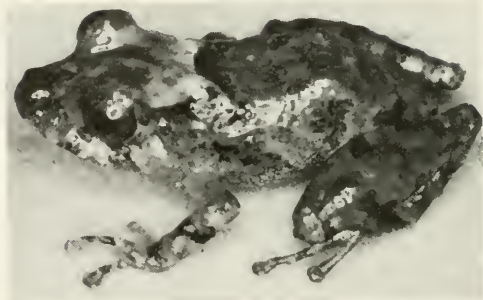


FIG. 55.—*Eleutherodactylus croceinguinis*, ♀, 20 mm SVL (KU 123454).

Materials.—Lago Agrio, 1; Puerto Libre, 24; Puerto Ore, 4; Santa Cecilia, 115.

Identification.—This small species of *Eleutherodactylus* differs from all other species in the area, except *E. variabilis*, in having a bright yellow spot in the groin and on the proximal part of the anterior surface of the thigh. In *E. croceinguinis* the spot is deep yellow to pale orange, and the spots do not approach the midline, whereas in *E. variabilis* the spots are pale yellow, large, narrowly bordered with black, and confluent, or nearly so, midventrally. Moreover, *E. croceinguinis* has a more robust body and tubercular skin on the dorsum, and *E. variabilis* has a more slender body and finely granular skin on the dorsum. *Eleutherodactylus croceinguinis* superficially resembles some individuals of *E. martiae*, which is readily distinguished from *E. croceinguinis* by the absence of yellow inguinal spots. *Eleutherodactylus altamazonicus* is like *E. croceinguinis* in having tubercular skin dorsally, but the groin and posterior surfaces of the thighs are barred or mottled with black or dull red.

The snout is round in dorsal view and in profile. The tympanum is concealed. The skin on the dorsum is tubercular, and that on the venter is granular. The discs on the fingers are about thrice the width of the digits and are truncate. The dorsal ground color is tan or brown with

dark brown to olive-brown markings consisting of an irregular interorbital bar, a transverse or shallow W-shaped mark on the scapular region, short transverse or diagonal marks on the body, and transverse bars on the limbs. Canthal and postorbital stripes are absent. A narrow middorsal cream or orange stripe is present in some individuals. Dark brown diagonal bars are present on the lips. The flanks are gray or tan. A large deep yellow to orange spot in the inguinal region is confluent or not with another spot on the proximal anterior surface of the thigh. The venter is gray with white flecks. The iris is dull bronze with dense black reticulations. ♂ 16 mm; ♀ 23 mm.

Occurrence.—This species is a forest dweller. Thirteen individuals were found on the forest floor by day, whereas 114 were on leaves and branches of bushes less than 1.5 m above the ground at night. *Eleutherodactylus croceinguinis* seems to be primarily nocturnal; all mating was observed at night. Those individuals found by day were inactive until disturbed.

Life History.—One hundred and three gravid females were found throughout the year; only 12 non-gravid females were found—March (1), May (1), July (6), August (2), September (1), December (1). Eighty-six gravid females had snout-vent lengths of 18.0–23.0 ($\bar{X}$ = 20.3) mm and contained 2–7 ($\bar{X}$ = 4.8) ovarian eggs no larger than 2.8 mm in diameter. Eleven amplexant pairs were found in March (2), April (3), May (3), June (2), and October (1). Two pairs deposited clutches of 6 and 4 unpigmented eggs in the laboratory on 25 October 1971 and 22 March 1972. The eggs were 3.4 mm in diameter. Juveniles having snout-vent lengths of 12.0–13.0 mm were found in March, April, July, and August; these seem to be too large to be recent hatchlings. Breeding obviously occurs throughout the year. Eggs probably are deposited on the ground.

Mating Call.—The call consists of a short click-like sound.

Food.—Identifiable food items were found in 24 stomachs. Spiders were the most common item (45.8% of the stomachs), followed by orthopterans (41.6%), beetles (20.8%), and ants (16.7%).

Eleutherodactylus diadematus

(Jiménez de Espada)

(FIGURE 56)

Hylodes diadematus Jiménez de la Espada, 1875, Vert. Viaj. Pacíf. Verif. Batr., Lisboa: pl. 3, fig. 3 [Type locality.—Unknown].

Eleutherodactylus diadematus—Gorham, 1966, Das Tierreich, Berlin, 85:69.

Material.—Lago Agrio, 17; Puerto Libre, 5; Santa Cecilia, 13.

Identification.—This species of *Eleutherodactylus* has diagonal dark brown or black markings on a yellowish tan to a bluish white ground color on the flanks and inguinal region. In this manner it resembles the smaller *E. altamazonicus*, a species differing from *E. diadematus* by having a pointed snout, tubercular skin on the dorsum, and dark brown venter; *E. diadematus* has a round snout, smooth skin with scattered pustules on the dorsum, and a pale venter with dark reticulations. Some individuals of *E. diadematus* have orange flecks on the posterior surfaces of the thighs. Other species having flecks or spots on the posterior surfaces of the thighs either have no dorsal pustules (*E. conspicillatus* and *E. lanthanites*) or have non-expanded tips of the fingers (*E. sulcatus*).

The snout is round in dorsal view and profile; an external tympanum is present. The discs on the fingers are expanded to thrice the width of the digits and are truncate. The skin on the dorsum is smooth with scattered pustules, and that on the venter is granular. The dorsum is tan, gray, or rusty brown with darker brown markings consisting of longitudinal marks extending posteriorly from the eyelids to the scapular region, an irregular transverse mark in the scapular region, and diagonal marks extending posterolaterally onto the flanks. The groin



FIG. 56.—*Eleutherodactylus diadematus*, ♂, 26 mm SVL; Cordillera del Dué, Provincia Napo, Ecuador (KU 123764).

and the proximal anterior and dorsal surfaces of the thighs are bluish white to yellowish tan with diagonal dark brown bars in the groin and transverse bars on the limbs. The posterior surfaces of the thighs are dark brown. Canthal and post-orbital stripes are absent; dark brown bars are present on the lips. The venter is creamy white with a greenish tint posteriorly; brown dashes or mottling are present on the throat and the belly. The iris is greenish bronze with a median horizontal red streak. ♂ 28 mm; ♀ 45 mm.

Occurrence.—*Eleutherodactylus diadematus* is an arboreal species occurring in primary (60%) and secondary (40%) forests. One was found on the forest floor by day; 11 were obtained by day when trees were felled, and 20 were perched on bushes and branches at night.

Life History.—Only nine adult females are in the collection. Three of six found in May and two of three in July were gravid. These had snout-vent lengths of 40.0–45.0 ($\bar{X}$ = 42.4) mm and contained 43–108 ($\bar{X}$ = 61.6) ovarian eggs, the largest of which had a diameter of 3.0 mm. One amplexant pair was found on a bush in July. Two juveniles having snout-vent lengths of 13.0 and 14.0 mm were found in July and August. One pair deposited eggs in the laboratory

on 9 May 1969; the 18 unpigmented eggs were 3.9 mm in diameter. Reproduction may be cyclic in this species. Because of its arboreal habits, eggs likely are to be deposited in bromeliads or amidst other epiphytes.

Mating Call.—The call is unknown.

Food.—Only 11 stomachs contained food. Roaches were by far the most common food item, appearing in 36.4 percent of the stomachs. These were followed by beetles (27.3%), spiders (18.2%) and ants (18.2%).

Eleutherodactylus lacrimosus (Jiménez de la Espada)

(FIGURE 57)

Cyclocephalus lacrimosus Jiménez de la Espada, 1875, Vert. Viaj. Pacif. Verif. Batr., Lisboa: pl. 3, fig. 5 [Type locality.—Unknown].

Eleutherodactylus lacrimosus—Gorham, Das Tierreich, Berlin, 85:80.

Material.—Lago Agrio, 2; Puerto Libre, 14; Santa Cecilia, 43.

Identification.—This small species with a flat head and proportionately large eyes has rounded expanded discs on the digits and can be mistaken for a *Hyla*. The absence of webbing in *E. lacrimosus* immediately distinguishes it from any hyloid with which it might be confused. Labial bars are absent in *E. lacrimosus*, *acuminatus*, *pseudoacuminatus*, and *quaquaversus*. Both *E. acuminatus* and *quaquaversus* have concealed tympana; *E. lacrimosus* has dorsal dark markings, which are absent in *E. pseudoacuminatus*.

The snout is round in dorsal view and truncate in profile. An external tympanum is present. The terminal discs on the fingers are round and about twice the width of the digit. The skin on the dorsum is smooth; that on the belly is granular. The dorsum is yellow, tan, olive green, or reddish brown with darker brown markings consisting of an inter-orbital stripe and one or more marks on the body. In some individuals these consist of transverse bars or chevrons. In others there is a large, elongate, irregu-



FIG. 57.—*Eleutherodactylus lacrimosus*, ♀, 25 mm SVL: Mera, Provincia Pastaza, Ecuador (KU 119513).

lar, middorsal mark. Narrow canthal and postorbital stripes are present or absent. Labial bars are absent. Faint transverse bars are evident on the limbs in some individuals. The flanks and anterior and posterior surfaces of the thighs are tan. Some individuals have the snout, rump, or heels creamy yellow, orange, or pale green. The venter is creamy yellow. The iris is bronze with a median horizontal red streak, which can diffuse to give the iris a copper color. ♂ 23 mm; ♀ 29 mm.

Occurrence.—With the exception of one individual on the forest floor by day, all specimens of *E. lacrimosus* were found on bushes and trees at night; only 4 percent were above 1.5 m. Fifteen individuals were in primary forest; 37 were in secondary forest.

Life History.—Gravid and non-gravid females were found only in February and April through September. Eleven females had snout-vent lengths of 20.0–29.0 ($\bar{X}$ = 23.5) mm and contained 7–16 ($\bar{X}$ = 9.5) ovarian eggs. The largest eggs were 2.5 mm in diameter. Amplectant pairs were found on low vegetation in June (1) and September (2). One pair deposited seven eggs, 4.5 mm in diameter, in the laboratory on 23 September 1971. Reproductivity activity is evident through most of the year; thus, I suspect that *E. lacrimosus* breeds throughout the year, with the possible exception of November–January. Oviposition sites are unknown, but because of the arboreal habits, it is likely that *E. lacrimosus* deposits eggs in bromeliads.

Mating Call.—The call consists of a single peep, repeated at intervals of a minute or more.

Food.—Among 17 stomachs containing food, small beetles were the most common food item (41.2% of stomachs), followed by orthopterans (29.4%) and spiders (23.5%).

Eleutherodactylus lanthanites Lynch

(FIGURE 58)

Eleutherodactylus lanthanites Lynch, 1975, Contr. Sci. Los Angeles Co. Mus., 272:10 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 9; Puerto Libre, 50; Santa Cecilia, 286.

Identification.—This is one of three species of *Eleutherodactylus* in the area having smooth skin on the venter. This species and *E. conspicillatus* have expanded terminal discs on the digits and dorsolateral dermal folds; *E. conspicillatus*, has a black face (side of head anterior to orbit), a creamy white throat, and orange or red flecks on a dark brown ground color on the posterior surfaces of the thighs, whereas *E. lanthanites* has a pale canthal stripe bordered below by a narrow brown stripe and a pale brown face, a gray throat with a median white streak, and pale creamy tan flecks on brown ground color on the posterior surfaces of the thighs. The only other species having smooth skin on the venter is *E. nigrovittatus*, which lacks dorsolateral folds and expanded discs. Three other species (*E. altamazonicus*, *diadematus*, and *sulcatus*) have pale spots on the posterior surfaces of the thighs, but in these species the spots are large, and the skin on the belly is granular.

The snout is narrowed anteriorly and rounded, barely projecting beyond the margin of the jaw. The skin is finely tuberculate above and smooth below; dorsal tubercles are absent, but narrow, low dorsolateral dermal folds are present. The discs on the fingers are expanded, truncate, and about two and one-half times the width of the digit. An external

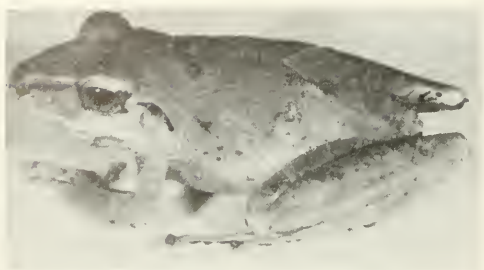


FIG. 58.—*Eleutherodactylus lanthanites*, ♀, 39 mm SVL (KU 146144).

tympanum is present. The dorsal ground color is olive-tan, grayish-tan, or pinkish brown with darker brown markings. The markings are highly variable but usually consist of an interorbital bar, a chevron or X-shaped mark in the scapular region, and two or three chevrons or transverse marks on the posterior part of the body. There usually is a pair of small black spots in the scapular region. The limbs are marked with brown transverse bars that are slightly narrower than the interspaces. A narrow creamy white or yellowish tan canthal stripe usually is evident; this is bordered below by a narrow dark brown stripe; a narrow dark brown or black postorbital stripe usually terminates above the tympanum. In most individuals the lips are barred tan or gray and dark brown, but some have a creamy white labial stripe. The dorsolateral folds are yellowish or pinkish tan; the flanks are paler than the dorsum and marked with tan or olive-gray vertical or diagonal marks, which may or may not be confluent with the dorsal markings. The groin and anterior surfaces of the thighs are pale orange to pale rose, whereas the posterior surfaces are brown with small, irregular yellowish tan (nearly orange in some individuals) flecks. The throat is gray with white flecks and a broad medial white stripe; the belly is creamy white with gray flecks, and the ventral surfaces of the thighs are greenish cream with brown flecks. The iris is bronze, clear above and with radiating black streaks below and a median horizontal red streak. ♂ 29 mm; ♀ 46 mm.

Occurrence.—*Eleutherodactylus lanthanites* is the most common and conspicuous forest-dwelling *Eleutherodactylus* in the area and is about equally abundant in primary and secondary forest. Ninety-eight individuals were found on the forest floor by day; one was in a small stream by day. Three individuals were on the ground at night, and 171 were on vegetation at night; of these, only 11 were at heights of more than 1.5 m. This species is active on the ground by day and on low vegetation at night.

Life History.—One hundred and five females containing mature ovarian eggs were found throughout the year, except September, when only two non-gravid individuals were found. Sixty-eight females had snout-vent lengths of 34.0–46.0 ($\bar{X}$ =38.7) mm and contained 20–52 ($\bar{X}$ =30.4) ovarian eggs, the largest of which had a diameter of 3.2 mm. One amplexant pair found on a bush on 2 April 1972 laid 30 eggs having diameters of 4.0 mm in the laboratory. The three smallest juveniles (10.0–11.0 mm in snout-vent length) were found in June and July. Certainly the species breeds throughout the year. Probably eggs are deposited on the ground as they are in other members of the *Eleutherodactylus fitzingeri* group.

Mating Call.—The call is unknown.

Food.—In 25 stomachs examined, orthopterans were present in 92 percent; beetles and spiders each were present in 20 percent. One fly, one ant, and one millipede completed the diets.

Eleutherodactylus martiae Lynch

(FIGURE 59)

Eleutherodactylus martiae Lynch, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 31:2 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 7; Puerto Libre, 51; Santa Cecilia, 57.

Identification.—This species is like *E. acuminatus*, *E. croceoguinis*, and *E. quaquaversus* in not having a visible



FIG. 59.—*Eleutherodactylus martiae*, amplexant pair, ♂, 18 mm SVL (KU 123815); ♀, 23 mm SVL (KU 123816).

tympanum. Among these species, *E. acuminatus* is readily distinguished by its uniform green dorsum and bold black canthal stripe. *Eleutherodactylus martiae* has scattered pustules on the dorsum and low dorsolateral dermal folds; the lips are barred, and tubercles are absent on the heels. In contrast, *E. quaquaversus* has a smooth dorsum without dorsolateral folds, no bars on the lips, and a small, pointed tubercle on each heel. *Eleutherodactylus croceinguinis* has tubercular skin on the dorsum and bold yellow or orange spots in the groin. *Eleutherodactylus martiae* superficially resembles *E. ockendeni* and *E. paululus*, both of which have an external tympanum; *E. ockendeni* usually has an H- or W-shaped arrangement of dermal ridges in the scapular region, and *E. paululus* has smooth skin without pustules on the dorsum.

The snout is acutely rounded in dorsal view and round in profile. The discs on the fingers are expanded, about twice the width of the digit, and broadly rounded. The skin on the belly is granular. The dorsum is dark brown with irregular transverse or longitudinal tan marks. In some individuals the heels are tan. The dorsal markings are highly variable. Although most individuals have a dark brown interorbital bar, in some it is tan, and others lack an interorbital mark-

ing. Narrow dark brown bars are present on the limbs. The groin and the anterior and posterior surfaces of the thighs are pale orange to tan, with or without faint brown bars. A narrow, diffuse, dark brown canthal stripe is evident in some individuals. Dark brown bars are present on the lips, and a narrow black post-orbital stripe expends posteroventrally from the eye. The ventral surfaces are gray or graying brown with small white to pale orange flecks. The iris is bronze with a median horizontal brown streak. ♂ 21 mm; ♀ 25 mm.

Occurrence.—*Eleutherodactylus martiae* is a nocturnal forest inhabitant that seeks diurnal shelter amidst leaf litter. All individuals were in the forest—24 in primary forest and 79 in secondary forest. Seven were in leaf litter on the forest floor by day, and 96 were on low vegetation (< 1.5 m) at night.

Life History.—Females containing mature ovarian eggs were found in every month, except April and December, months in which no females were found. Eighteen females having snout-vent lengths of 19.0–23.0 ($\bar{X}$ = 21.7) mm contained 5–13 ($\bar{X}$ = 7.8) ovarian eggs, the largest of which was 2.0 mm in diameter. Ten amplexant pairs were found on low vegetation in seven months (January, March, May–August, November). Four pairs deposited eggs in the laboratory; clutches contained 8, 8, 9, and 10 unpigmented eggs having diameters of 3.2, 3.5, 3.2, and 3.7 mm, respectively. Two of eight eggs deposited on 4 June hatched on 30 June; hatchlings had snout-vent lengths of 5.0 mm. This species obviously breeds throughout the year. Presumably the egg clutches are placed amidst leaf litter on the forest floor.

Mating Call.—The call consists of a series of short clicks.

Food.—A diversity of small arthropods was present in 25 stomachs. Orthopterans were present in 48.0 percent of the stomachs, followed by beetles (16.0%), flies (16.0%), homopterans (12.0%), and lepidopteran larvae (12.0%).



FIG. 60.—*Eleutherodactylus nigrovittatus*, ♀, 26 mm SVL (KU 123503).

Eleutherodactylus nigrovittatus

Andersson

(FIGURE 60)

Eleutherodactylus nigrovittatus Andersson, 1945, Ark. Zool., 37A(2):42 [Type locality.—Abitagua, Provincia Pastaza, Ecuador].

Material.—Lago Agrio, 1; Puerto Libre, 5.

Identification.—This is one of three species of *Eleutherodactylus* in the area having smooth skin on the venter. The other two species (*E. conspicillatus* and *E. lanthanites*) have dorsolateral dermal folds and long fingers with expanded terminal discs, whereas *E. nigrovittatus* has short fingers without expanded terminal discs and lacks dorsolateral folds. The only other species of *Eleutherodactylus* having short fingers without expanded discs is *E. sulcatus*, a larger species with a broad head ($> 50\%$ of snout-vent length), numerous longitudinal ridges on the dorsum, tubercles on the eyelids, and granular skin on the venter. *Eleutherodactylus nigrovittatus* can be easily confused with *Adenomera andreae*; the latter differs from *E. nigrovittatus* by having pustular skin on the dorsum, more pointed snout in dorsal view and profile, absence of a dark anal patch, and presence of a dark triangular mark on the occiput. *Eleutherodactylus*

nigrovittatus has smooth skin on the dorsum, a dark anal patch, and no triangular mark on the occiput.

The snout is broadly rounded in dorsal view and truncate in profile. The skin is smooth on the dorsum and venter; dorsal tubercles and folds are absent. The digits are short and lack expanded discs; an external tympanum is present. The dorsum is reddish tan to pale brown with dark brown transverse bars on the limbs and dark brown or black longitudinal dashes dorsolaterally on the body. Canthal and postorbital stripes are absent. The upper lips are barred with dark brown and white or pale tan. The forelimbs and flanks are orange-tan; creamy white mottling is present on the flanks in one individual. A dark brown inguinal spot is present in most specimens. The subanal region is dark brown; distally the posterior surfaces of the thighs are tan. The ventral surfaces are pale gray with minute white flecks. The iris is dull bronze suffused with black, giving an overall gray appearance. ♂ 19 mm; ♀ 22 mm.

Occurrence.—The limited data on six specimens agree with more extensive observations on this species in the Cordillera del Dué to the west of Santa Cecilia. The species is active by day on the forest floor. One was found in primary forest, five in secondary forest; one was sitting on the ground at night, and the others were active by day.

Life History.—Four adult females were found, one in May, and three in July; the latter all had snout-vent lengths of 22.0 mm and contained 9-10 ($\bar{X}=9.3$) ovarian eggs 2.5 mm in diameter. Data are insufficient to determine the seasonality of breeding. Presumably eggs are deposited on the ground.

Mating Call.—The call is unknown.

Food.—Four individuals had eaten 9 ants, 2 spiders, 2 beetles, 2 orthopterans, one beetle larva, and one annelid worm.

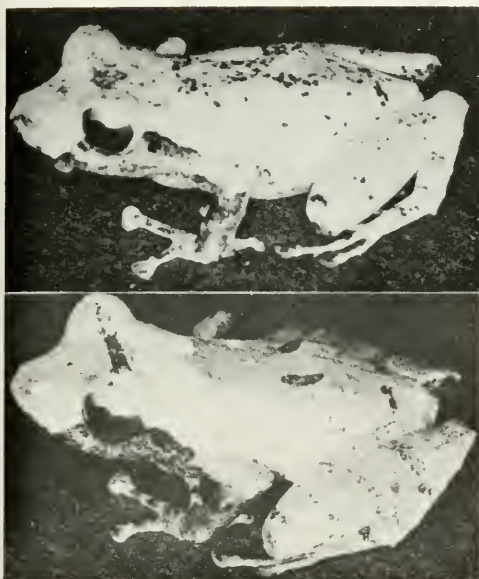


FIG. 61.—*Eleutherodactylus ockendeni*. Upper: ♀, 27 mm SVL (KU 126213). Lower: ♂, 20 mm SVL (KU 126214).

Eleutherodactylus ockendeni (Boulenger)

(FIGURE 61)

Hylodes ockendeni Boulenger, 1912, Ann. Mag. Nat. Hist., (8)10:187 [Type locality.—La Unión, Río Huacamayo, Carabaya, Departamento Puno, Perú].

Eleutherodactylus ockendeni—Gorham, 1968, Das Tierreich, 85:89.

Material.—Dureno, 1; Lago Agrio, 6; Puerto Libre, 22; Puerto Ore, 6; Santa Cecilia, 127.

Identification.—Most individuals of this species have W- or H-shaped tubercular ridges in the scapular region; otherwise the skin on the dorsum is smooth. Some individuals of *E. croceoinguinis* have a shallow W-shaped series of folds in the scapular region; elsewhere the skin on the dorsum is tubercular. Many short ridges are present on the back of *E. sulcatus*, and in some individuals the ridges form an H-shaped pattern in the scapular region, but *E. sulcatus* has short slender digits and a broad head ($>50\%$ of snout-vent length), whereas *E. ockendeni* has long digits with expanded discs and a narrow head ($\pm 35\%$

of snout-vent length). Young individuals of *E. ockendeni* or specimens having poorly developed scapular patterns can be confused with *E. paululus*, which lacks a scapular arrangement of tubercular ridges but has dark canthal and post-orbital stripes and a pale gold iris with a black horizontal stripe. Canthal and postorbital stripes are absent in *E. ockendeni*, in which the iris is metallic green above and red below or green with a median horizontal red streak.

The snout is round in dorsal view and truncate in profile. An external tympanum is present. The terminal discs on the fingers are expanded about two and one-half times the width of the digit and are truncate. The skin on the belly is granular; with the exception of an H- or W-shaped arrangement of tubercles in the scapular region, the skin on the dorsum is smooth. The dorsum varies from tan to reddish brown with dark brown markings consisting of H- or W-shaped marks corresponding to the tubercles in the scapular region, one or two narrow transverse marks post-sacally, and transverse bars on the limbs. Some individuals have a brown interorbital bar, and others have a pair of small dorsolateral spots in the scapular region. Canthal and postorbital dark stripes are absent. Dark brown bars are present on the lips, but these are faint in some individuals. The flanks are paler than the dorsum, plain, or marked with irregular brown spots. The anterior and posterior surfaces of the thighs are brown to rose-red. The venter is pale gray. In most individuals the iris is metallic green; the lower half is red or a median horizontal red streak is present. In some individuals the upper part of the iris is bronze. ♂ 21 mm; ♀ 29 mm.

Occurrence.—Data on 141 specimens reveal that this strictly forest-inhabiting frog is active on the forest floor by day and on low vegetation at night. About half (53%) of the frogs were in primary forest. Twenty-seven frogs were found on the forest floor by day, and three

were on the ground at night. Of 111 found on vegetation at night, only three were at heights of more than 1.5 m.

Life History.—Thirty-six females containing mature ovarian eggs were found throughout the year, except September and November through January. Non-gravid females were obtained in every month except January. Twenty-nine gravid females had snout-vent lengths of 23.0–29.0 ($\bar{X}$ = 26.4) mm and contained 5–18 ($\bar{X}$ = 13.0) ovarian eggs. The largest eggs were 2.8 mm in diameter. Four clasping pairs were found in April (2), May (1), and June (1). Apparently breeding takes place throughout the year, with the possible exception of November–January. Eggs probably are deposited amidst leaf litter on the forest floor.

Mating Call.—The call consists of two notes, “aah-aah.”

Food.—In 25 stomachs, orthopterans were found in 68.0%, followed by spiders (24.0%), beetles (12.0%), and ants (8.0%).

Eleutherodactylus orphnolaimus Lynch

(FIGURE 62)

Eleutherodactylus orphnolaimus Lynch, 1970, Proc. Biol. Soc. Washington, 83:221 [Type locality.—Lago Agrio, Provincia Napo, Ecuador].

Material.—Lago Agrio, 2.

Identification.—This is one of two species in the area having tubercles on the eyelid. The other species, *E. sulcatus*, has a broad head (> 50% of snout-vent length), dermal ridges on the dorsum, and short fingers lacking expanded discs. *Eleutherodactylus orphnolaimus* has a much narrower head, no dermal ridges on the dorsum, and long fingers with expanded discs.

The snout is pointed in dorsal view and in profile; the tip of the snout projects well beyond the margin of the lip. An external tympanum is present. The discs on the fingers are expanded, two and one-half times the width of the digit,



FIG. 62.—*Eleutherodactylus orphnolaimus*, ♂, 24 mm SVL (KU 125332).

and truncate. The skin on the dorsum is smooth, and that on the belly is granular. The dorsum is tan to grayish tan, with or without a suffusion of pale green, with a narrow brown interorbital bar and two narrow brown chevrons on the body. Faint brown labial bars and narrow transverse bars on the limbs are evident. Dark brown canthal and postorbital stripes are present. The flanks are brown. The groin and anterior and posterior surfaces of the thighs are reddish orange. The belly is brown with white flecks, and the throat is brown with tan streaks. The iris is pale bronze, with or without a pinkish suffusion dorsally, and a median horizontal reddish brown streak. ♂ 24 mm; ♀ 34 mm.

Occurrence.—Both specimens were obtained on the ground immediately after large trees had been felled in primary forest. These observations and the enlarged terminal discs on the toes suggest that the species is arboreal.

Life History.—No data are available. The single female, obtained in May, showed no evidence of reproductive activity.

Mating Call.—The call is unknown.

Eleutherodactylus paululus Lynch

(FIGURE 63)

Eleutherodactylus paululus Lynch, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 31:6 [Type locality.—Lago Agrio, Provincia Napo, Ecuador].

Material.—Lago Agrio, 4; Puerto Libre, 1; Santa Cecilia, 5.



FIG. 63.—*Eleutherodactylus paululus*, ♂, 16 mm SVL (KU 126208).

Identification.—This small species has smooth skin on the dorsum, expanded discs on the digits, and a dull green dorsum. Two other *Eleutherodactylus* in the area are green dorsally; *E. acuminatus* has a concealed tympanum and a black canthal stripe, and *E. pseudoacuminatus* has a narrow snout and narrower digits than *E. paululus*. The species resembles small individuals of *E. ockendeni*, most of which have H- or W-shaped tubercular ridges in the scapular region. Furthermore, *E. paululus* has dark canthal and postorbital stripes (absent in *E. ockendeni*) and a pale gold iris with a median horizontal black stripe (metallic green and red in *E. ockendeni*). The coloration of *E. paululus* is similar to that of *E. martiae*, which differs by having a concealed tympanum and scattered pustules on the dorsum. *Eleutherodactylus corceinguinis* superficially resembles *E. paululus* but differs by having tubercular skin on the dorsum and large yellow spots in the groin. The latter character is shared with *E. variabilis*, which has smooth skin on the dorsum.

The snout is round in dorsal view, shallow and truncate in profile. An external tympanum is present. The discs on the fingers are expanded, about twice the width of the digits, and truncate. The skin on the dorsum is smooth, that on the belly granular. The dorsum is dull green

or greenish gray, with or without a tan suffusion laterally, with reddish brown or grayish black markings consisting of a narrow interorbital stripe, narrow canthal and postorbital stripes, faint labial bars, a blotch or W-shaped mark in the scapular region, one or two chevrons or pair of spots posteriorly on the body, and narrow transverse bars on the limbs. The flanks are pale gray or tan, plain or marked with the posterolateral ends of dorsal chevrons. The anterior and posterior surfaces of the thighs are grayish tan. The proximal posterior surfaces of the thighs are brown. The venter is pale green with small white flecks on the belly. The iris is pale bronze to gold with a median horizontal brown or black streak. ♂ 16 mm; ♀ 21 mm.

Occurrence.—Four individuals were amidst leaf litter on the ground in primary forest by day; four were on low bushes in secondary forest, and one was on a bush in a clearing, all at night. These limited data suggest that the species is nocturnal and a forest inhabitant.

Life History.—Adult females were found in March-May and July-August. One each from March and May were gravid. Each had a snout-vent length of 19.0 mm and contained five ovarian eggs 2.0 mm in diameter. One female from each of March and May was in amplexus. The data are too scanty for conclusions regarding seasonality of breeding. Presumably eggs are laid on the forest floor.

Mating Call.—The call is unknown.

Food.—Eight individuals had eaten 7 flies, 2 beetles, 1 homopteran, and 1 spider.

Eleutherodactylus pseudoacuminatus Shreve

(FIGURE 64)

Eleutherodactylus pseudoacuminatus Shreve, 1935, Occas. Papers Boston Soc. Nat. Hist., 8:218 [Type locality.—Sarayacu, Provincia Pastaza, Ecuador].

Material.—Lago Agrio, 9; Puerto Libre, 7; Puerto Ore, 1; Santa Cecilia, 23.



FIG. 64.—*Eleutherodactylus pseudoacuminatus*, ♀, 21 mm SVL (KU 126164).

Identification.—This is one of three species of green *Eleutherodactylus* in the area; *E. acuminatus* is a larger species having the tympanum covered with skin and having a black stripe from the snout through the eye. In *E. pseudoacuminatus* and *paululus* the tympanum is visible externally, and a black canthal stripe is absent. *Eleutherodactylus paululus* differs from *E. pseudoacuminatus* by having a broader snout and broader discs on the fingers. Other small green frogs in the area are centrolenids and hylids, all of which have extensive webbing between the toes; webbing is absent in *E. pseudoacuminatus*.

The snout is narrow and rounded. The skin on the dorsum is smooth; that on the belly is granular; dorsal tubercles and folds are absent. The discs on the fingers are slightly expanded ($1.5 \times$ digit) and round. Usually the dorsum and the anterior and posterior surfaces of the thighs are uniform pale green to grayish green. Some individuals have a tan suffusion, especially middorsally. In a few individuals, a narrow creamy white canthal stripe is present. Two specimens had creamy yellow dorsolateral stripes, and one had a cream snout. Small black flecks are present on the dorsum in some individuals. The venter and flanks are white. The iris is pale bronze with a median, horizontal red stripe. ♂ 19 mm; ♀ 23 mm.

Occurrence.—Frogs of this species are found in about equal abundance in

primary and secondary forest. Three were obtained from bromeliads by day, and two were on the ground at night. All others were on vegetation at night; only four of those were at heights of more than 1.5 m.

Life History.—Fourteen gravid females were obtained throughout the year: February (3), March (1), May (3), July (4), August (2), December (1). Twelve gravid females having snout-vent lengths of 18.0–22.0 ($\bar{X}=20.8$) mm contained 4–11 ($\bar{X}=7.3$) ovarian eggs having diameters of 3.0 mm. Four of these females were in amplexus (February, March, May and December). One female deposited 7 unpigmented eggs 3.5 mm in diameter in the laboratory on 17 December. Two of the eggs hatched on 15 January; both hatchlings had snout-vent lengths of 5.0 mm. Apparently *E. pseudoacuminatus* breeds throughout the year. Oviposition sites are unknown, but the fact that this orboreal species inhabits bromeliads, suggests that eggs may be deposited in bromeliads.

Mating Call.—The mating call is a soft, buzz-like peep.

Food.—Only 11 stomachs contained food. Small beetles were found in 36.4 percent of the stomachs, followed by flies (27.3%), ants (18.2%), homopterans (18.2%), and spiders (18.2%).

Eleutherodactylus quaquaversus Lynch

(FIGURE 65)

Eleutherodactylus quaquaversus Lynch, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 31:9 [Type locality.—South slope of Cordillera del Dué, above Río Coca, 1150 m, Provincia Napo, Ecuador].

Material.—Puerto Libre, 3; Santa Cecilia, 10.

Identification.—This is one of three species of *Eleutherodactylus* in which the tympanum is not visible. Among the three species, *E. acuminatus* is readily distinguished by its uniformly green dorsum and bold black canthal stripe. *Eleutherodactylus quaquaversus* has smooth



FIG. 65.—*Eleutherodactylus quaquaversus*. Upper: ♂, 23 mm SVL; Cordillera del Dué, Provincia Napo, Ecuador (KU 123746). Middle: ♀, 31 mm SVL; Cordillera del Dué, Provincia Napo, Ecuador (KU 123749). Lower: ♂, 22 mm SVL; 17.5 km NNE Santa Rosa, Provincia Napo, Ecuador (KU 143441).

skin on the dorsum, no bars on the lips, and a pointed tubercle on the heel. By comparison, *E. martiae* has scattered pustules dorsally, dorsolateral dermal folds, bars on the lips, and no tubercle on the heel. The combination of a covered tympanum and a tubercle on the heel immediately distinguishes *E. quaquaversus* from other *Eleutherodactylus* in the area.

The snout is round in dorsal view and in profile. The discs on the fingers are about twice the width of the digits and truncate. The skin on the dorsum is smooth; that on the belly is granular. The dorsal ground color is dull red, tan, brown, or gray with irregular darker markings consisting of an interorbital bar, longitudinal dashes or transverse marks on the body, and transverse bars on the limbs. In darker colored individuals a narrow cream canthal stripe is evident. Although dark vertical bars are not present on the upper lips, one or two small dark spots are present in some individuals; others have one or two small white spots below the eye. A few individuals have a broad cream interorbital bar, and one has a cream snout. A post-orbital stripe usually is absent. The flanks are tan or pale gray; small dark flecks are present in some individuals. The groin and anterior and posterior surfaces of the thighs are purplish red with small white flecks. The venter is bronze-white, with small scattered black flecks in most individuals. The iris varies from silvery cream to green with a red tint below. ♂ 22 mm; ♀ 29 mm.

Occurrence.—This species is nocturnal in the forest; 9 of 13 individuals were in secondary forest. All were on low vegetation at night. These observations are corroborated by more extensive data from the Cordillera del Dué and Cordillera Umbaqui to the west of Santa Cecilia, where most of the specimens of this species have been collected.

Life History.—One gravid female from September, 29.0 mm in snout-vent length, contained 22 ovarian eggs 2.6 mm in diameter.

Mating Call.—The mating consists of a single high-pitched note.

Food.—A variety of small arthropods have been eaten by 13 individuals. Beetles were present in 35.3 percent of the stomachs, followed by orthopterans (29.4%), spiders (23.5%), lepidopteran larvae (11.8%), and ants (11.8%).



FIG. 66.—*Eleutherodactylus sulcatus*, ♀, 49 mm SVL (KU 123586).

Eleutherodactylus sulcatus (Cope)

(FIGURE 66)

Hylodes sulcatus Cope, 1874, Proc. Acad. Nat. Sci. Philadelphia, 26:126 [Type locality.—Nauta, Departamento Loreto, Perú].

Eleutherodactylus sulcatus—Gorham, 1966, Das Tierreich, Berlin, 85:103.

Material.—Lago Agrio, 6; Puerto Libre, 3; Santa Cecilia, 22.

Identification.—This toad-like *Eleutherodactylus* has a broad depressed head (> 50% of snout-vent length) with cranial ridges, short digits lacking expanded terminal discs, granular skin on the venter, tubercles on the eyelids, and longitudinal dermal ridges on the dorsum. The only other species of *Eleutherodactylus* in the area having short digits without expanded terminal discs is *E. nigrovittatus*, which has a narrower head, smooth skin on the venter, and no dermal ridges on the dorsum. The only other species having tubercles on the eyelids, *E. orphnolaimus*, has smooth skin on the dorsum and long fingers with expanded discs. *Ischnocnema quixensis* also has a short, squat body, but it differs from *E. sulcatus* by having a narrower head, tubercular skin on the dorsum, and small light flecks on the posterior surfaces of the thighs. All other species of *Eleutherodactylus* with pale spots on the posterior surfaces of the thighs have ex-

panded discs on the fingers. True toads (*Bufo*) have paratoid glands.

The snout is broad and rounded in dorsal view, depressed and round in profile. The skin on the venter is granular; that on the dorsum is smooth with scattered small tubercles and short, longitudinal dermal ridges, which tend to form an H-shaped pattern in the scapular region in most individuals. An external tympanum is present. The dorsum is dull gray or reddish tan with or without irregular small dark brown marks or larger markings consisting of an inter-orbital bar, a blotch in the scapular region and one or two chevrons or transverse bars on the posterior part of the body. Narrow dark brown transverse bars are present on the limbs. The lips usually are boldly marked with dark brown bars. Canthal and postorbital stripes are absent. The flanks are pale gray or pinkish tan. The groin and the anterior and posterior surfaces of the thighs are dark brown to black with large cream spots. The venter is grayish cream; the throat is noticeably darker in some individuals. The ventral surfaces of the hands and feet are dull orange. The iris is greenish silver, reticulated with black. ♂ 35 mm; ♀ 54 mm.

Occurrence.—This large, terrestrial *Eleutherodactylus* occurs only in forests, where individuals have been found active or amidst leaf litter by day. Three were found on the forest floor by day. Ten of 26 specimens were taken in primary forest.

Life History.—Of eight adult females, only one (collected in July) was gravid; it had a snout-vent length of 49.0 mm and contained 32 ovarian eggs 2.5 mm in diameter. One juvenile having a snout-vent length of 11.0 mm was found in March, and two having lengths of 13.0 mm were found in May. Presumably eggs are deposited on the ground.

Mating Call.—The call is unknown.

Food.—A variety of terrestrial arthropods was included in the diets of 15 individuals. Orthopterans were found in

53.3 percent of the stomachs, beetles in 20.0 percent, centipedes in 20.0 percent, and millipedes in 13.3 percent.

Eleutherodactylus variabilis Lynch

(FIGURE 67)

Eleutherodactylus variabilis Lynch, 1968, J. Herp., 2:129 [Type locality.—Limoncocha, Provincia Napo, Ecuador].

Material.—LAGO Agrio, 2; Puerto Libre, 49; Santa Cecilia, 268.

Identification.—This is one of two species of *Eleutherodactylus* in the area having large yellow spots in the groin. In *E. variabilis* the spots (one on each side) are pale yellow, narrowly bordered by black, and confluent, or nearly so, midventrally. The other species, *E. croceinguinis*, has deep yellow or orange spots that do not approach the midline. Furthermore, in *E. variabilis* the body is more robust, and the skin on the dorsum is finely granular, whereas in *E. croceinguinis* the body is more robust, and the skin on the dorsum is tubercular.

The snout is narrow and rounded in dorsal view and in profile; an external tympanum is present. The discs on the fingers are truncate and about twice the width of the digits. The skin on the dorsum is finely granular (shagreened); that on the belly is granular. The dorsal coloration is highly variable, ranging in color from tan to brown, gray, red, or green. Most individuals have a pattern of darker markings consisting of a narrow interorbital bar and transverse or diagonal markings on the body and limbs; the markings on the body usually extend onto the flanks. In some individuals the dorsum is uniform tan, green, or dull red, with or without darker longitudinal streaks; in these individuals the flanks are brown or gray. A few individuals have a narrow middorsal cream or yellow stripe. Canthal and postorbital stripes are absent or dark brown, when present. Dark brown diagonal bars are present on the lips. A large pale yellow spot extends from the inguinal region



FIG. 67.—*Eleutherodactylus variabilis*. Upper: ♀, 21 mm SVL (KU 111168). Lower: ♀, 23 mm SVL (KU 111140).

onto the proximal anterior surface of the thigh. Usually the spot has a narrow black border. The spots on either side are confluent, or nearly so, midventrally. The posterior surfaces of the thighs are dull red, rose-pink, or gray. The ventral surfaces are cream with brown or gray flecks. The iris is bronze with a median horizontal reddish brown streak. ♂ 19 mm; ♀ 27 mm.

Occurrence.—*Eleutherodactylus variabilis* apparently is a “weed” species most frequently encountered in disturbed areas. Only five individuals were found by day – three on the ground in primary forest (two where trees were being felled), one amidst leaf litter in secondary forest, and one on the ground in a clearing after a rain. All others were found at night on low vegetation – secondary forest (210), primary forest (16), swamp (21), clearing (3), banana grove (1). Observations made in 1971-72 indicate that *E. variabilis* is especially abundant in partially cleared forest and in forest-edge habitats.

Life History.—No fewer than six gravid females were found in any given

month; 195 of the 289 females contained mature ovarian eggs. One hundred and forty-eight gravid females having snout-vent lengths of 22.0-27.0 ($\bar{X}$ =24.4) mm contained 2-11 ($\bar{X}$ =6.7) ovarian eggs having diameters up to 3.0 mm. Amplectant pairs were found on low vegetation in March (3), April (1), May (1), June (2), August (1), October (1), and November (1). Six captive pairs deposited eggs in the laboratory. In clutches of 5, 6, 7, 7, 7, and 11 unpigmented eggs, the diameters of the eggs were 3.8, 4.0, 4.0, 3.9, 3.8, and 4.0 mm, respectively. Obviously this species breeds throughout the year. Possibly the eggs are deposited amidst leaf litter or beneath detritus on the forest floor or amidst debris in bushes or low trees.

Mating Call.—The call consists of a series of soft clicks.

Food.—Orthopterans were found in 38.4 percent of 26 stomachs; ants, flies, beetles, and spiders were each found in 15.4 percent. Hemipterans, homopterans, and beetle larvae also were included in the diets.

Ischnocnema quixensis

(Jiménez de la Espada)

(FIGURE 68)

Oreobates quixensis Jiménez de la Espada, 1872, An. Soc. Espan. Hist. Nat., Madrid, 1:87 [Type locality.—"Quito, Ecuador"].

Ischnocnema quixensis—Lynch, 1971, Misc. Publ. Mus. Nat. Hist. Univ. Kansas, 53:156.

Material.—Dureno, 1; Lago Agrio, 7; Puerto Libre, 9; Puerto Ore, 1; Santa Cecilia, 106.

Identification.—This robust toad-like species has large tubercles on all dorsal surfaces of the body. It differs from toads of the genus *Bufo* by having tubercles on the head and by lacking bony cranial crests. Among the many species of *Eleutherodactylus* in the area, *Ischnocnema* can be confused only with *E. sulcatus*, which has a smooth dorsum with longitudinal dermal ridges. Small individuals of *Ischnocnema* might be mistaken for *Physalaemus petersi*, another

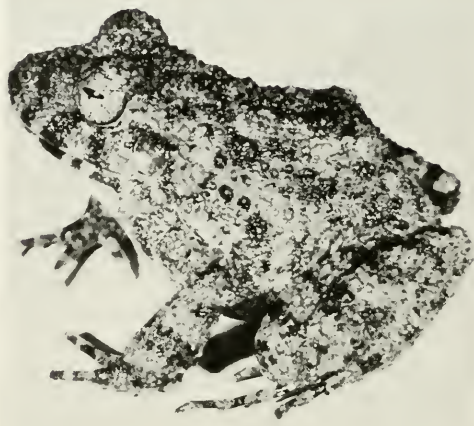


FIG. 68.—*Ischnocnema quixensis*, ♀, 55 mm SVL (KU 146174).

er toad-like species with black spots in an orange groin.

The snout is acutely rounded in dorsal view and round in profile. An external tympanum is present. The fingers and toes are moderately long, unwebbed, not expanded terminally and bear large conical subarticular tubercles. The skin on the dorsum is tubercular; that on the belly is smooth. The dorsum varies from pinkish brown to olive-brown with dark brown to reddish brown markings consisting of a broad interorbital bar, a chevron or H- or W-shaped mark in the scapular region, irregular spots or transverse marks elsewhere on the back, vertical bars on the lips, and broad transverse bars on the limbs. The flanks are brown; some individuals have a pinkish tint in the inguinal region. The anterior and posterior surfaces of the thighs are brown. The ventral surfaces are brown to grayish brown with white mottling. The iris is coppery bronze. ♂ 48 mm; ♀ 59 mm.

Occurrence.—This frog primarily is a nocturnal forest dweller. Of 91 specimens, only 24 were obtained by day; of these, six were under logs, 16 were in leaf litter, and two were in a small stream. A juvenile was sitting on a low herb at

night; otherwise all other individuals were on the ground. Two of the frogs were in clearings and one in a banana grove; all others were in forest (primary 23%, secondary 77%).

Life History.—Gravid females were found in every month except January and October. Thirty-four females having snout-vent lengths of 47.0–59.0 ($\bar{X}$ = 52.9) mm contained 15–51 ($\bar{X}$ = 35.1) ovarian eggs having diameters up to 4.1 mm. Juveniles having snout-vent lengths of 11.0–14.0 mm were found in January, March, June, and July. Thus, it seems that this species breeds throughout the year. Previously the life history of *Ischnocnema* has been unknown. Although the present data are not conclusive, I believe that it is safe to assume that *Ischnocnema quixensis* is like *Eleutherodactylus* in depositing clutches of terrestrial eggs that undergo development directly into small frogs. This assumption is based on the small clutch size, large ovum size, and lack of pigment in the eggs.

Mating Call.—The call consists of a series of low-pitched guttural notes.

Food.—Examination of 26 stomachs revealed the presence of orthopterans in half of the stomachs. Other major food items were beetles (11.5%) and millipedes (11.5%), whereas spiders, beetle larvae, and ants were each present in only two stomachs. Each of the following were found in only one stomach: hemipteran, lepidopteran larva, and gastropod.

***Leptodactylus discodactylus* Boulenger**

(FIGURE 69)

Leptodactylus discodactylus Boulenger, 1883, Proc. Zool. Soc. London, 1883:637 [Type locality.—Yurimaguas, Departamento Loreto, Perú].

Material.—Santa Cecilia, 26.

Identification.—*Leptodactylus discodactylus* and *L. wagneri* differ from the other species of *Leptodactylus* in the area by having lateral fringes on the toes.



FIG. 69.—*Leptodactylus discodactylus*, ♀, 33 mm SVL (KU 143518).

These two species differ in that *L. discodactylus* has expanded, round, terminal discs on the digits and usually a dark throat and cream belly, whereas *L. wagneri* lacks expanded terminal discs on the digits and has a cream throat and belly, both mottled with brown. Furthermore, *L. discodactylus* is smaller (< 36 mm) than *L. wagneri* (< 78 mm). *Leptodactylus discodactylus* is most easily confused with *Adenomera andreae*, a smaller species (< 28 mm) lacking lateral fringes on the toes and having the first two fingers equal in length; the first finger is longer than the second in *L. discodactylus*. The other species of *Leptodactylus* in the area, except *L. wagneri*, have distinct dorsolateral dermal folds. The presence of short toes with basal webbing distinguishes *L. discodactylus* from *Eleutherodactylus*, and the expanded discs and little webbing distinguish it from *Rana*.

The dorsum is dark brown, and the flanks are grayish brown or reddish tan, usually with a brown spot in the groin and one or two brown spots on the flank. A narrow pinkish cream or gray inter-orbital bar usually is evident. The side of the head is dark brown, usually with four narrow, diagonal or vertical cream bars (two below orbit, one below nostril, and one between nostril and orbit); another cream bar is present on the tip of the snout. The limbs are dark brown with darker transverse bars barely evident in some specimens. The posterior

surfaces of the thighs are brown; black flecks are evident distally in some specimens. The throat is dark brown with cream flecks, and the belly and ventral surfaces of the limbs are cream with brown flecks laterally. The iris is bronze with brown reticulations. Some adults of both sexes have bright yellow glandular areas laterally on the body. Breeding males lack nuptial pads or spines. ♂ 29 mm; ♀ 35 mm.

Occurrence.—All individuals of *Leptodactylus discodactylus* were found in forest. Two were resting on low vegetation at night, two were in a swamp at night, and one was on the forest floor at night. Nineteen individuals were found by day; all of these were in swampy areas. Although all but three were near water, only two were in water. The small sample of *L. discodactylus* is from March-October with no specimens from May and September and 15 specimens from July. My general impression is that this frog is restricted to swamp forest, where it probably is active throughout the year.

Life History.—Six females having 148-420 ($\bar{X}$ =234.8) mature ovarian eggs were found in April (2), June, July (2), and October; the maximum diameter of the eggs is 1.2 mm. Heyer and Bellin (1973) noted that at Limoncocha, Ecuador, male *L. discodactylus* called day and night after heavy rains and that they did not call during rainless periods or times of light rain. The smallest juveniles (7.3-7.7 mm in snout-vent length) were found in July. These limited data suggest that *L. discodactylus* may be a sporadic opportunistic breeder, whose breeding activity is associated with periods of heavy rainfall. At such times depressions in the forest are filled with water and form suitable breeding sites.

Tadpoles.—No tadpoles of this species were found at Santa Cecilia, but tadpoles are available from Mera, Provincia Pastaza, Ecuador, where they were obtained in a shallow forest-edge swamp. The following description is based on

KU 121362 (tadpoles in stage 30). The body length is 10 mm, and the total length is 25 mm. The body is ovoid, widest and deepest posteriorly; the snout is bluntly rounded in dorsal view and acutely rounded in profile. The eyes are small, close together, and directed dorso-laterally. The nostrils are about two-fifths the distance from the tip of the snout to the eyes. The spiracle is sinistral; the opening is directed posterodorsally at a point just below the midline at midlength of the body. The mouth is ventral. The lips have lateral folds; the median part of the upper lip is bare; elsewhere there is a single row of labial papillae. There are two upper and three lower rows of denticles; all are complete. The beaks are slender and finely serrate. The dorsal and ventral fins are equal in depth and slightly shallower than the caudal musculature at midlength of the tail. The dorsal fin does not extend onto the body and is deepest at about two-fifths of the length of the tail. The tip of the tail is acutely rounded. The body is brown with white flecks ventrally. The caudal musculature is dull brown, and the fins are tan.

Mating Call.—A recording of *Leptodactylus discodactylus* made at Limoncocha, Ecuador, generously was provided by W. R. Heyer. The call consists of a series of short notes "wheet, wheet, wheet" produced at a rate of 44 notes per minute. The dominant frequency of the notes is at about 3000 Hz.

Food.—Of eight stomachs containing food, five contained eight beetles comprising 41 percent of the bulk. Two contained one homopteran each, representing 8.7 percent of the bulk. Other food items were represented by one individual each and included Diptera, Orthoptera, formicid, Hemiptera, Isopoda, and Annelida.

Taxonomic Comments.—Heyer (1974b) suggested that this species is generically distinct from *Leptodactylus* and proposed for it the generic name *Vanzolinius*.



FIG. 70.—*Leptodactylus mystaceus*, juvenile, 17 mm SVL (KU 122555).

Leptodactylus mystaceus (Spix)

(FIGURE 70)

Rana mystacca Spix, 1824, Spec. Testud. Ran. Brasil., Monaco: 27 [Type locality.—Bahia and Solimoes, Brasil].

Leptodactylus mystaceus—Mehely, 1904, Ann. Mus. Hungar., Budapest, 2:219.

Material.—Lago Agrio, 2; Puerto, 1; Santa Cecilia, 114+21.

Identification.—This species of *Leptodactylus* is readily distinguished from other frogs in the area by its acuminate snout and distinct creamy white labial stripe. The only other *Leptodactylus* having a pale labial stripe is *L. rhodomystax*, in which the stripe is pinkish tan. Also, *L. rhodomystax* has a blunt snout and a dark venter; the venter in *L. mystaceus* is creamy white. *Leptodactylus mystaceus* is like other members of the genus, except *L. discodactylus* and *wagneri*, in lacking lateral fringes on the toes. *Leptodactylus mystaceus* has dorsolateral dermal folds, a character shared with *L. pentadactylus*, *L. rhodomystax*, *L. rhodonotus*, and *Rana palmipes*. The white labial stripe and cream belly immediately distinguish *L. mystaceus* from all of these frogs, and basal webbing between the toes serves as an additional difference from *Rana palmipes*, which has extensive webbing. *Leptodactylus mystaceus* frequently is mistaken as an *Eleutherodactylus*, but no species of *Eleutherodactylus* in the area (except variants of *E. lathanites*, which

have expanded discs on the digits) has a white labial stripe and dorsolateral folds.

The dorsum is gray, olive-tan, or reddish tan with darker brown or grayish brown blotches consisting of a triangular mark with the apex posteriorly on the head and usually three crude chevron-shaped marks middorsally. The hind limbs are colored like the body and have dark transverse bars; the forelimbs are paler than the body and usually have faint transverse bars on the forearms. The posterior surfaces of the thighs are mottled brown and black with a longitudinal cream stripe distally. The dorsolateral fold is dark brown with a cream streak on the medial edge posteriorly. The flanks are pale gray or tan. The side of the head, including the tympanic region, is black, sharply defined above by a narrow bronze-tan canthal stripe. A broad silvery white or creamy white labial stripe extends from the tip of the snout to the base of the arm. The venter is creamy white with brown flecks laterally on the throat and belly. The iris is bronze above and dark metallic reddish brown below. Breeding males lack nuptial pads or spines. ♂ 56 mm; ♀ 60 mm.

Occurrence.—*Leptodactylus mystaceus* was found throughout the year in primary forest (15%), secondary forest (50%), forest edge (5%), and clearings (30%). About one-third of the frogs were found by day in leaf litter or under logs. At night they were on the ground in forest or clearings, but 10 were found on low bushes (< 1.5 m), and two were in water in swamps. Most (84%) individuals were not near water.

Life History.—Males call throughout the year from secluded sites (under logs, under tree roots, in holes in the ground). Females bearing mature ovarian eggs were found in every month except April, June, September, and December; no females were found in June. Apparently

L. mystaceus breeds throughout the year. The unpigmented eggs are deposited in a foam nest; one nest about 100 mm in diameter and 50 mm in depth was in a cavity under a rock in a marshy clearing; others were found in weedy shallow water. Twenty-two females having snout-vent lengths of 52.0-60.0 ($\bar{X}$ =54.8) mm contained 171-425 ($\bar{X}$ =280.5) eggs, the largest having a diameter of 2.4 mm. Nine recently metamorphosed young have snout-vent lengths of 14.0-15.5 ($\bar{X}$ =14.7) mm.

Tadpoles.—The following description is based on KU 109168, stage 27, having a snout-vent length of 9 mm and a total length of 26 mm. The body is ovoid, widest medially and flat ventrally. In dorsal view the snout is bluntly rounded, whereas in profile it is inclined anteroventrally and rounded below. The eyes are moderate in size, well separated from one another, and directed dorso-laterally. The nostrils are midway between the tip of the snout and the eyes. The spiracle is sinistral; the opening is directed posterodorsally at a point just below the midline at about two-thirds of the length of the body. The mouth is ventral and has lateral folds. The medium part of the upper lip is bare; elsewhere there is one row of labial papillae. There are two upper and three lower rows of denticles; the second upper row is interrupted medially. The beaks are slender and finely serrated. The dorsal and ventral fins are equal in depth and shallower than the caudal musculature. The dorsal fin does not extend onto the body and is deepest at midlength of the tail. The tip of the tail is pointed. The body is olive-tan; in large individuals (> stage 37) a dark brown dorsolateral stripe and an interorbital bar are evident. The venter is gray with gold flecks anteriorly. The tail is olive-tan with dull green and orange-yellow flecks and dark brown reticulations. The iris is golden bronze.

Tadpoles have been found in shallow grassy pools in clearings, in a *Heliconia*-

choked swamp in forest, and in a partially shaded pond at the edge of the forest. All tadpoles were observed in shallow water (< 25 cm), where they took refuge in grasses or amongst leaves on the bottom.

Mating Call.—The call consists of a series of notes "oit, oit, oit." Analysis of one recording made at Santa Cecilia reveals that the note repetition rate is 48 notes per minute with the dominant frequency at about 1500 Hz. and an emphasized harmonic at about 6000 Hz.

Food.—Sixteen of 26 frogs examined contained orthopterans, and 10 of these contained only orthopterans, which make up 81 percent of the bulk of the food. Individual beetles were present in six stomachs and represent 8 percent of the bulk. The other food items were single examples of a variety of small arthropods.

Leptodactylus pentadactylus (Laurenti)

(FIGURE 71)

Rana pentadactyla Laurenti, 1768, Synops. Rept., Wien: 32 [Type locality.—"Indiis"].
Leptodactylus pentadactylus—Nieden, 1923, Das Tierreich, Berlin, 46:472.

Material.—Durenó, 1; Lago Agrio, 2; Puerto Libre, 1; Santa Cecilia, 30+13.

Identification.—This large *Leptodactylus* is like *L. mystaceus*, *L. rhodomystax*, *L. rhodonotus*, and *Rana palmipes* in having distinct dorsolateral dermal folds. *Leptodactylus pentadactylus* usually has a reddish brown dorsum and has the toes webbed basally in contrast to *Rana palmipes*, which is grayish green dorsally and has extensive webbing between the toes. Of the aforementioned species of *Leptodactylus*, *L. mystaceus* and *L. rhodomystax* have pale labial stripes, whereas *L. pentadactylus* and *L. rhodonotus* have dark vertical bars on the lips. These two species differ in coloration and in the disposition of dermal folds. The dorsum in *L. pentadactylus* usually has distinct darker brown or reddish brown transverse blotches, whereas the dorsum in *L. rhodonotus* is uniform



FIG. 71.—*Leptodactylus pentadactylus*. Upper: ♀, 154 mm SVL (KU 146176). Lower: juvenile, 55 mm SVL (KU 122576).

dusky brown. The limbs in *L. pentadactylus* have distinct broad, transverse dark bars, but in *L. rhodonotus* only indistinct, narrow, transverse lines are present. Usually the posterior surfaces of the thighs are black with creamy yellow flecks in *L. pentadactylus* and uniform brown in *L. rhodonotus*. The dorsolateral fold in *L. rhodonotus* is continuous with the supratympanic fold, but in *L. pentadactylus* the dorsolateral fold extends posteriorly from the posterior edge of the eyelid and is distinct from the supratympanic fold, which extends diagonally onto the flank.

In most individuals the dorsum is orange-tan or grayish tan with five or six broad, transverse brown or reddish brown blotches between the dorsolateral folds. The dorsal surfaces of the limbs are tan or gray with distinct, broad,

transverse dark brown bars. A narrow black stripe extends from the snout through the nostril and eye to the upper edge of the tympanum. The lips are tan with four or five short, black vertical bars on the margin of the lip. The flanks are paler than the dorsum and marked by a few black spots. The posterior surfaces of the thighs are black with cream flecks. The venter is cream with bold dark brown mottling, especially on the belly and hind limbs. In some juveniles the dorsum is pale green with dark brown or black markings; the posterior surfaces of the thighs are black, and the belly is dark grayish brown with or without cream flecks. The iris is dark bronze. Breeding males have large nuptial spines on the prepollex and on the chest. ♂ 169 mm; ♀ 181 mm.

Occurrence.—*Leptodactylus pentadactylus* was found in primary forest. Most individuals were active on the ground at night, but two were in water. Juveniles were found amidst leaf litter or under logs by day.

Life History.—Males call sporadically throughout the year. Although some were observed to call from various terrestrial sites in the forest, most sounded as though they were calling from near the edge of the largest lake. Only ten adult females were found; none was gravid. Tadpoles were obtained in March-July. Small juveniles were taken in June, July, and November. These data are inconclusive with respect to seasonality of breeding.

Tadpoles.—The following description is based on KU 146771 (stage 32, body length 18.2 mm, total length 61.5 mm). The body is ovoid, widest at midlength and deepest posteriorly. The snout is bluntly rounded in dorsal view and round in profile. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are midway between the tip of the snout and the eyes. The spiracle is sinistral and directed posterodorsally at a point on the

midline at about three-fifths the length of the body. The mouth is anteroventral and lacks lateral folds. The median part of the upper lip is bare; elsewhere there is one row of labial papillae. There are two upper and three lower rows of denticles; the second upper row is broadly interrupted medially, and the third lower row is much shorter than the others. The tail is long (70% of total length), pointed terminally, and has low fins. The dorsal fin does not extend onto the body, is one-third deeper than the ventral fin, and three-fourths of the depth of the caudal musculature. The body is grayish brown with a brown interorbital bar; the venter is gray. The tail is brown with a creamy orange tint to the edge of the dorsal fin. The iris is bronze.

Tadpoles have been found in shallow temporary pools in clearings and in swamps in forests.

Mating Call.—The call consists of a series of loud notes, “whoop, whoop, whoop.” Some calls consist of only a few notes, whereas others consist of 20-30 notes, in which case the note repetition rate is 21 notes per minute. In one recording that was analyzed the dominant frequency was at about 3300 Hz.

Food.—These large frogs have a propensity for eating large arthropods. One contained the remains of a giant tarantula having a chelicera 9 mm in length; another contained a millipede 83 mm in length. Small frogs, crustaceans, and molluscs are taken in addition to a wide variety of insects (Table 5).

Taxonomic Comments.—Heyer (1972) named *Leptodactylus knudseni* on the basis of 33 juveniles from Limoncocha, Provincia Napo, Ecuador. The species was diagnosed as differing from *L. pentadactylus* by having green and black dorsal markings and uniformly dark posterior surfaces of the thighs. The largest specimen, the juvenile female holotype, has a snout-vent length of 63 mm.

I compared the holotype and six paratypes with specimens from Santa Cecilia. Like Heyer, I found no morphological

TABLE 5.—Food Analysis of *Leptodactylus pentadactylus*. (N=27)

PREY ITEM	Frequency	Frequency	Percent
	Frogs	Prey	Bulk
Orthoptera	20	25	42.4
Coleoptera	12	24	21.7
Diplopoda	6	9	10.7
Arachnida	3	3	6.8
Crustacea	1	2	3.3
Anura	1	2	3.3
Hemiptera	2	4	3.2
Isopoda	1	2	2.4
Lepidoptera			
(larvae)	2	2	2.2
Coleoptera			
(larvae)	2	2	1.9
Hymenoptera			
(formicids)	2	5	1.2
Dermaptera	1	1	0.4
Mollusca	1	1	0.4
Isoptera	1	1	0.1

differences between *L. knudseni* and *L. pentadactylus*. Three individuals from Santa Cecilia (snout-vent lengths of 37, 40, and 52 mm) have a pale green dorsal ground color with dark brown to black transverse blotches and black flanks and posterior surfaces of the thighs. Among 10 *knudseni*-like frogs, seven have uniformly grayish brown venters, whereas small cream spots are present on the venters of the other three. Of seven juveniles having the *pentadactylus*-like dorsal coloration, three have spots on the venter, and four are uniformly grayish brown. Also, three of these seven have uniformly dark posterior surfaces of the thighs.

Because of the various combinations of color characters occurring in the juveniles, the absence of morphological differences in differently patterned specimens, and the absence of adults having the green and black coloration, I am reluctant to recognize *Leptodactylus knudseni* as a species distinct from *L. pentadactylus*; instead it seems as though two color morphs occur in juvenile *L. pentadactylus*. A taxonomic revision of the *Leptodactylus pentadactylus* group is beyond the scope of this paper, especially since there is no biological evidence to support the recognition of more

than one species of *L. pentadactylus*-like frogs at Santa Cecilia.

***Leptodactylus rhodomystax* Boulenger**

(FIGURE 72)

Leptodactylus rhodomystax Boulenger, 1883, Proc. Zool. Soc. London, 1883:637 [Type locality.—Yurimaguas, Provincia Loreto, Perú].

Material.—Lago Agrio, 1; Puerto Libre, 1; Santa Cecilia, 3+2.

Identification.—This moderately large species resembles *Leptodactylus mystaceus*, *L. pentadactylus*, *L. rhodonotus*, and *Rana palmipes* in having distinct dorsolateral dermal folds. The presence of extensive webbing between the toes distinguishes *Rana palmipes* from *L. rhodomystax*, which has only basal webbing. *Leptodactylus pentadactylus* and *L. rhodonotus* have dark bars on the lips and thereby differ from *L. mystaceus* and *L. rhodomystax*, both of which have pale labial stripes. *Leptodactylus rhodomystax* has a blunt snout, pinkish tan labial stripe, dark venter, and pale flecks on the posterior surfaces of the thighs; *L. mystaceus* has an acuminate snout, creamy white labial stripe, cream venter, and a pale stripe on the posterior surface of each thigh.

The dorsum is reddish brown to grayish brown; the dorsolateral folds are dark brown. The flanks are orange-tan. The groin and posterior surfaces of the thighs are dark grayish brown with small pale greenish yellow spots. The side of the head, including the tympanic region, is dark brown. A pale pinkish tan labial stripe extends from the snout to the base of the arm. The throat is dark brown; the chest, belly, and ventral surfaces of the limbs are cream, heavily suffused with brown. The iris is dull bronze above and reddish bronze below. Breeding males have nuptial spines on the prepollex and chest. ♂ 90 mm.

Occurrence.—Three adult males were found at night in swamps at Santa Cecilia in March. One adult male was amidst leaf litter in mature forest at



FIG. 72.—*Leptodactylus rhodomystax*, ♀, 60 mm SVL (KU 122581).

Lago Agrio in May, and one small female was beneath a stone at the edge of a clearing at Puerto Libre in July.

Life History.—Except for one male calling in March, nothing is known.

Tadpoles.—Tadpoles tentatively identified as this species by W. R. Heyer were found in two swamps in forest in June, 1968. The following description is based on KU 124147 (stage 25, body length 6 mm, total length 21.3 mm). The body is ovoid, widest anteriorly and deepest posteriorly. The snout is truncate in dorsal view and round in profile. The eyes are large, widely separated, and directed laterally. The nostrils are about one-third the distance from the tip of the snout to the eyes. The spiracle is sinistral; the opening is directed posterodorsally at the midline and about two-thirds of the length of the body. The mouth is anteroventral and has no lateral folds. The median part of the upper lip is bare; elsewhere there is a single row of labial papillae. There are two upper and three lower rows of denticles; the second upper row is widely separated medially, and the third lower row is much shorter than the others. The tail is 72 percent of the total length and terminates in a filamentous tip. The dorsal fin is shallow, one third the depth of the ventral fin, deepest at midlength of the tail, where it is about equal to the depth of the caudal musculature, and does not extend onto the body. The body and

caudal musculature are brownish gray, and the tail is marked with irregular darker flecks.

Mating Call.—Unfortunately the call was neither recorded nor described.

Food.—Three individuals contained two roaches (Blattidae), one grasshopper (Orthoptera), and one millipede (Diplopoda).

Leptodactylus stenodema

Jiménez de la Espada

(FIGURE 73)

Leptodactylus stenodema Jiménez de la Espada, 1875, Vert. Viaje Pacifico, p. 64 [Type locality.—San José de Motí, Provincia Napo, Ecuador]. Pyburn and Heyer, 1975, Copeia, 3:585.

Material.—Puerto Libre, 1.

Identification.—This species has a robust body and short limbs. It is like *L. mystaceus*, *L. pentadactylus*, *L. rhodomystax*, and *Rana palmipes* in having distinct dorsolateral dermal folds. *Leptodactylus stenodema* has a reddish brown dorsum and the toes basally webbed, in contrast to *Rana palmipes*, which has a grayish green dorsum and the toes extensively webbed. *Leptodactylus stenodema* and *L. pentadactylus* have dark labial bars, whereas *L. mystaceus* and *L. rhodomystax* have pale labial stripes. *Leptodactylus stenodema* differs from *L. pentadactylus* in coloration and in the disposition of the dorsolateral folds. In the former the dorsum is uniform dull reddish brown, and the venter is grayish tan, whereas in *L. pentadactylus* the dorsum usually is orange or reddish tan with distinct transverse dark brown blotches, and the venter is cream mottled with brown. The dorsolateral fold is continuous with the supratympanic fold in *L. stenodema*; the dorsolateral fold is medial to the supratympanic fold in *L. pentadactylus*.

The dorsum is dull reddish brown, becoming orange-brown just medial to the black dorsolateral fold. The dorsal surfaces of the limbs are dark brown with indistinct narrow black transverse



FIG. 73.—*Leptodactylus stenodema*, ♂, 94 mm SVL (KU 122582).

lines. The posterior surfaces of the thighs are black. The side of the head is brown, and the lip is orange-brown with four triangular black marks. The flanks are dull brown above and orange-brown below. The throat is dark brown, and the other ventral surfaces are grayish tan. The iris is bronze with a median horizontal red streak. Breeding males have nuptial spines on the prepollex. ♂ 94 mm.

Occurrence.—The single adult male was sitting on the ground in secondary forest at night.

Life History.—Nothing is known.

Mating Call.—According to Pyburn and Heyer (1975), the call is “a ‘whoop’ emitted while the frog sits in a burrow somewhat removed from the entrance.”

Leptodactylus wagneri (Peters)

(FIGURE 74)

Plectromantis wagneri Peters, 1862, Monatsb. Akad. Wiss. Berlin, 1862:232 [Type locality.—West side of Andes of Ecuador]. *Leptodactylus wagneri*—Nieden, 1923, Das Tierreich, Berlin, 46:479.

Material.—Lago Agrio, 6; Puerto Libre, 1; Santa Cecilia, 118+3.

Identification.—This *Leptodactylus* is like *Adenomera andreae* and *L. discodactylus* in lacking dorsolateral dermal folds; all other species of *Leptodactylus* in the area have dorsolateral folds. *Leptodactylus wagneri* and *L. discodactylus* differ from *Adenomera* in having the

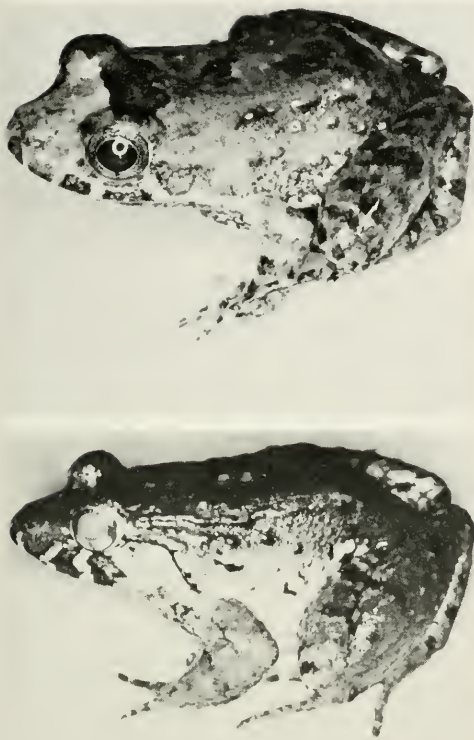


FIG. 74.—*Leptodactylus wagneri*. Upper: juvenile, 19 mm SVL (KU 119343). Lower: ♂, 45 mm SVL (KU 122584).

first finger longer than the second (equal in *Adenomera*), and in having lateral fringes on the toes (absent in *Adenomera*). *Leptodactylus discodactylus* differs from *L. wagneri* by having expanded, round, terminal discs on the digits and usually a dark throat and cream belly, whereas *L. wagneri* lacks expanded terminal discs and has a cream throat and belly, both mottled with brown. Furthermore, *L. wagneri* is larger (> 78 mm) than *L. discodactylus* (< 36 mm).

The snout is rounded. The skin on the dorsum has numerous small spicules and many short elongate ridges laterally. The dorsum and flanks vary from dull olive-green to brown or gray with dark brown to black irregular spots or mottling. Usually there is a crudely triangu-

lar-shaped mark, with the apex directed posteriorly, on the head. This is narrowly bordered by cream or pale gray. The lips are barred with cream and dark brown. The dorsal surfaces of the limbs are colored like the body and have indistinct, irregular, darker transverse bars. The posterior surfaces of the thighs are black with greenish yellow to yellowish tan flecks or spots. The venter is dull creamy white with brown or dark gray mottling, most prominent in larger individuals. The iris is dull bronze with a median horizontal grayish brown streak. Some adults of both sexes have prominent yellow glandular areas ventrolaterally, and breeding males have two nuptial spines on the prepollex. ♂ 59 mm; ♀ 77 mm.

Occurrence.—*Leptodactylus wagneri* was found in all months except September and December through February. Although it was not found commonly in any given habitat, it occurred in a wide variety of habitats, exclusive of the river edge. One-third of the specimens were found in clearings, usually at night; other places of occurrence were marshes and swamps (25%), primary forest (12%), secondary forest (10%), streams (10%), and lakes (3%). Of eight specimens found by day, three were in small streams in forest and five were under cover in clearings.

Life History.—Calling males were heard in a forest swamp in July. Gravid females were found in March, May, and June at which times 40, 50, and 50 percent, respectively, of captured females were gravid. Non-gravid females were found in April, July, and August. Seven gravid females 51.0–77.0 ($\bar{x}=67.3$) mm in snout-vent length contained 1000–3150 ($\bar{x}=1588.6$) ovarian eggs. The lightly pigmented eggs are deposited in foam nests in temporary ponds and ditches.

Tadpoles.—The following description is based on KU 146773 (stage 27, body length 12.0 mm, total length of 34.5 mm). The body is ovoid, and widest and deepest at midlength. In dorsal

view and in profile the snout is round. The eyes are moderately large, broadly separated, and directed dorsolaterally. The nostrils are about midway between the tip of the snout and the eyes. The spiracle is sinistral; the opening is directed posterodorsally at a point just below midline at about midlength of the body. The mouth is anteroventral and has shallow lateral folds. The median part of the upper lip is bare; there is one row of labial papillae laterally and two rows ventrally. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially. The beaks are moderately slender and weakly serrated. The dorsal and ventral caudal fins are equal in depth; each is about one-half the depth of the caudal musculature at midlength of the tail, the point of greatest depth of the tail. The dorsal fin does not extend onto the body, and the tip of the tail is acutely rounded. The body is dark brown with white flecks laterally; the tail is cream with brown flecks on the caudal musculature, dorsal fin, and anterior half of ventral fin.

Tadpoles were found amidst dense vegetation in a shallow, weed-choked pond in March, and in a semi-permanent pond in May.

Mating Call.—The call consists of a series of soft, high-pitched notes: "oit, oit, oit." Analysis of one recording male at Belém, Brasil, reveals that the note repetition rate is 68 notes per minute with the dominant frequency at about 2700 Hz and emphasized harmonics at about 5400 and 8100 Hz.

Food.—Twenty-five individuals contained a variety of insects, one gastropod, one chilopod, one crustacean, one spider, and one frog (*Hyla brevifrons*). Ants were eaten by 12 frogs, orthopterans by 11, and beetles by 9; these items constituted 12, 27, and 14 percent of the bulk, respectively. The largest prey item was a centipede 47 mm long in a frog having a snout-vent length of 69 mm. Another individual having a snout-vent length of

54 mm had eaten a caterpillar 33 mm long.

***Lithodytes lineatus* (Schneider)**

(PLATE 1)

Rana lineata Schneider, 1799, Hist. Amphib., 1:138 [Type locality.—Guyana].

Lithodytes lineatus—Fitzinger, 1843, Syst. Rept., Wien, 1:31.

Material.—Lago Agrio, 3; Puerto Libre, 8; Santa Cecilia, 2.

Identification.—This brightly colored frog with a black dorsum and yellow to tan dorsolateral stripes can be confused only with some dendrobatids, all of which have scutes on the dorsal surfaces of the terminal segments of each digit. Of these dendrobatids, *Dendrobates pictus* and *Phyllobates* resemble *L. lineatus* in having dorsolateral light stripes, but both have mottled venters; in *D. pictus* the dorsolateral stripes are narrow, and a lateral white stripe is present in *P. femoralis*. *Lithodytes* has a large red inguinal spot and another red spot on the posterior surface of the thigh; red spots are lacking in the dendrobatids.

The dorsum and flanks are black. A pair of broad dorsolateral stripes originate on the tip of the snout and extend along the edge of the eyelid to the groin; the stripes are creamy yellow in juveniles and golden tan in adults. The dorsal surfaces of the limbs are pale brown with dark brown transverse marks. A large red spot is present in the inguinal region and proximal anterodorsal surface of the thigh; another large red spot is present on the posterior surface of the thigh. The venter is grayish brown with creamy yellow flecks laterally. The iris is deep bronze with brown bars. ♂ 45 mm; ♀ 56 mm.

Occurrence.—The terrestrial species apparently is active by day and night. Three were in primary forest, nine in secondary forest, and one at the edge of the forest. Eight were active on the ground by day and four by night; one was sitting on a log at night.

Life History.—Two females (May and July) contained 195 and 230 ovarian eggs. The number of eggs is excessive in comparison with *Eleutherodactylus* of similar body size; thus it seems unlikely that *Lithodytes* has terrestrial eggs with direct development. Perhaps they construct aquatic foam nests and have aquatic larvae.

Mating Call.—The call is unknown.

Food.—Nine individuals contained a variety of small insects. Ants were present in seven stomachs, fly larvae in three, coleopterans, hemipterans, and orthopterans in two; and termites in one.

Remarks.—The coloration of *Lithodytes* sufficiently resembles that of the poisonous *Phylllobates femoralis* that the former could be considered a mimic and the latter the model. The resemblance is particularly striking in juvenile *Lithodytes*. Both species are terrestrial forest inhabitants from the Guianas to Perú; however, *Lithodytes* is active by day and night, whereas *Phylllobates* is diurnal.

Physalaemus petersi
(Jiménez de la Espada)

(FIGURE 75)

Engystomops petersi Jiménez de la Espada, 1872, An. Soc. Espan. Hist. Nat., Madrid, 1:86 [Type locality.—"Oriente," Ecuador].
Physalaemus petersi—Lynch, 1970, Copeia, 1970(3):492.

Material.—Puerto Libre, 5; Santa Cecilia, 13.

Identification.—Resembling a small toad with a pointed snout, *Physalaemus petersi*, differs from *Bufo* by lacking cranial crests and parotoid glands and from *Dendrophryniscus* by having tubercles on the dorsum and a black and white mottled belly.

The skin on the dorsum is bedecked with numerous, small, red or orange tubercles that are in contrast to the dull brown ground color. A single dark brown bar traverses the thigh and shank. Some individuals have small, dark brown spots on the dorsum. The flanks are creamy



FIG. 75.—*Physalaemus petersi*, ♂, 24 mm SVL; Mera, Provincia Pastaza, Ecuador (KU 120-280).

yellow anteriorly, becoming orange posteriorly in larger individuals, with large black spots; the anterior and posterior surfaces of the thighs are mottled black and cream. The posterior part of the belly and ventral surfaces of the thighs are white or gray with bold black mottling. The throat and chest are dark gray with minute white flecks and, usually, a narrow median cream line; some individuals have faint orange mottling on the throat and chest. The iris is dull bronze. ♂ 26 mm; ♀ 32 mm.

Occurrence.—Although toads of the genus *Physalaemus* usually are nocturnal, some observations at Santa Cecilia seem to contradict this generality. Eight individuals were found on the forest floor; two of these were amidst leaf litter by day, whereas the others were active at night. Seven individuals (juveniles and subadults) were found (sleeping?) on leaves of low herbs (< 30 cm) at night. All calling males (three) were found at night. M. L. Crump (pers. com.) found juveniles on low vegetation but adults breeding at night at Belém, Brasil, and J. D. Lynch (pers. com.) found males calling at night at Mera, Ecuador. The limited observations suggest a possible difference in diel activity cycles between adults and juveniles; at

least adults are active at night. About equal numbers of individuals were found in primary and secondary forest.

Life History.—One gravid female collected in July contained 340 eggs. Males were heard calling only in July from shallow water in temporary ponds. Presumably this species, like other *Physalaemus*, constructs a foam nest on the surface of ponds.

Tadpoles.—No tadpoles were found at Santa Cecilia; the following description is based on specimens (KU 121357) from Mera, Provincia Pastaza, Ecuador. A typical tadpole in developmental stage 28 has a body length 13.7 mm and a total length of 31.5 mm. The body is robust, widest posteriorly and about as deep as wide. The snout is narrow and rounded. The eyes are small, close together, and directed dorsolaterally. The nostrils are closer to the eyes than to the tip of the snout. The spiracle is directed postero-dorsally; the spiracular opening is at a point just below midline about one-third the length of the body. The caudal fins are deeper than the moderately robust caudal musculature, deepest at mid-length of the tail, and rounded at the tip; the dorsal fin does not extend onto the body. The mouth is anteroventral, about as wide as the anterior part of the body. The upper lip is bare; elsewhere there is one row of blunt labial papillae. The beaks are broad, slender, and weakly serrate. There are two upper and three lower rows of denticles; the upper rows are slightly longer than the lower rows, and the second upper row is narrowly interrupted medially. The body and caudal musculature are pale brown with dark brown markings on the dorsum of the body and large brown spots on the tail. The dorsal markings usually consist of a pair of spots on the snout, a broad blotch posterior to the eyes and a narrow transverse bar posteriorly on the body. The caudal fins are translucent with brown flecks on the dorsal fin; flecks are absent in small tadpoles and most numerous in larger ones.

Tadpoles have been found in shallow open ponds, where they seek refuge in the mud on the bottom.

Mating Call.—Males call while floating on the surface of the water. The call is a series of two or three notes: “doo-ing, doo-ing.”

Food.—Six individuals contained food: 7, 9, 9, 23, 43, and 55 termites.

Remarks.—The range of *Physalaemus petersi* has been poorly documented. I have examined specimens (KU) from many localities from Departamento Putumayo, Colombia, southward through Ecuador and Perú to Departamento Cochabamba, Bolivia, and from Belém, Brasil.

BUFONIDAE

Bufo glaberrimus (Günther)

(FIGURE 76)

Bufo glaberrimus Günther, 1868, Proc. Zool. Soc. London, 1868:483 [Type locality.—“Bogota,” Colombia].

Material.—Puerto Libre, 1; Santa Cecilia, 6.

Identification.—This toad differs from all other *Bufo* in the area by lacking cranial crests and tubercles on the dorsum. These characters, in combination with dark flanks and venter and pale dorsum, immediately distinguish *Bufo glaberrimus* from other toads and toad-like anurans in the area.

The skin on the dorsum is smooth, except for scattered, low pustules in large individuals; the skin is smooth on the throat and chest and weakly granular on the belly and thighs. The parotoid glands are ovoid and about twice the length of the eyelid. The toes are about one-third webbed; the distal two and one-half segments of the fourth toe are not included in the web. The dorsum is orange-tan to olive-tan; the pustules are reddish brown in some individuals. The sides of the head and flanks are dark brown, and the venter is grayish brown with cream spots. The iris is pale gold with black reticulations. ♂ 72 mm.

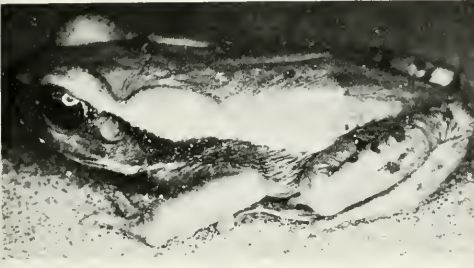


FIG. 76.—*Bufo glaberrimus*, ♀, 40 mm SVL (KU 120339).

Occurrence.—Ecological data are available for only three specimens. An adult male was in a hole in a clearing by day. One juvenile was under a log in a clearing by day, and one juvenile was at the edge of the river at night. I suspect that *Bufo glaberrimus* is like *B. guttatus* and inhabits more open forests than typical of the Santa Cecilia area.

Life History.—Nothing is known.

Mating Call.—The call is unknown.

Food.—Three individuals had eaten 27 ants, eight beetles, one termite, one millipede, and one whip scorpion (Pseudoscorpionida).

Taxonomic Comments.—Stebbins and Hendrickson (1959:515) and Rivero (1961:20) treated *Bufo glaberrimus* as a subspecies of *Bufo guttatus*, Schneider, but Cochran and Goin (1970:113) considered it to be a full species. Too little material is available from the upper Amazon Basin to determine the taxonomic status of the members of the *Bufo guttatus* complex occurring there.

Bufo marinus (Linnaeus)

(FIGURE 77)

Rana marina Linnaeus, 1758, Syst. Nat., Ed. 10, 211 [Type locality.—“Americas”].

Bufo marinus—Schneider, 1799, Hist. Amphib., 1:219.

Material.—Puerto Libre, 2; Puerto Ore, 3; Santa Cecilia, 49+8.

Identification.—Adults of *Bufo marinus* can be distinguished from other toads in the area solely by their enormous size. Characteristically juveniles



FIG. 77.—*Bufo marinus*, ♀, 125 mm SVL; Belém, Estado do Pará, Brasil (KU 128735).

and subadults have dark spots or mottling on the tubercular dorsum. The large trianguloid parotoid gland and low cranial crests distinguish *B. marinus* from other toads. Cranial crests are absent in *B. glaberrimus*, as are warts on the dorsum. The supratympanic crests are greatly expanded dorsolaterally in adult *B. typhonius*. The crest between the eye and the tip of the snout is straight in *B. marinus*, whereas it extends posteriorly from the snout and then angles laterally to the anterior corner of the orbit in *B. typhonius*. The combination of cranial crests, tubercles on the dorsum, and webbing between the toes distinguish juvenile *B. marinus* from *Dendrophryniscus minutus* and small *Ischnocnema quixensis* and *Eleutherodactylus sulcatus*.

The skin on the dorsum is tubercular; that on the venter is granular. In adults the tips of the tubercles are keratinized. Adults have distinct, moderately low, keratinized cranial crests and huge, trianguloid parotoid glands that are twice the length of the eyelids and extend ventrally to the level of the jaw. The toes are more than one-half webbed; the distal two segments of the fourth toe are free of webbing. The dorsum varies from grayish tan to olive-brown or reddish brown with or without small darker spots, which are indistinct or absent in

most large adults. The margin of the upper lip is creamy tan. The venter is creamy white with grayish brown spots. The iris is pale green suffused with black. Breeding males have horny nuptial excrescences on the thumb and in some individuals the excrescences also occur on the second and third fingers. ♂ 127 mm; ♀ 146 mm.

Occurrence.—Only two specimens were found in the forest; all others were in clearings and along the Río Aguarico. Many individuals were observed nightly on the airstrip. By day juveniles were found beneath logs in clearings. Males called from small temporary pools in clearings or pools in the river bank left by the receding river.

Life History.—Five of six adult females contained mature ovarian eggs; these were found in March (1), July (1), August (2), and October (1). Females having snout-vent lengths of 115, 130, and 146 mm contained 4240, 9100, and 12,700 eggs respectively. Males call throughout the year, but most frequently they are heard on nights when there has been little or no rain. Eggs are deposited in long strings in shallow temporary pools in clearings and in pools in the river bank. Five recently metamorphosed young from June have snout-vent lengths of 11.9-12.7 ($\bar{x}$ =12.4) mm.

Tadpoles.—The following description is based on tadpoles in developmental stage 30 (KU 109186) having a body length of 10.3 mm and a total length of 26.0 mm. The body is ovoid, widest just behind the eyes and deepest at midlength. The snout is bluntly rounded in dorsal view and round in profile. The eyes are moderately large, narrowly separated, and directed dorsolaterally. The nostrils are at about 60 percent of the distance from the tip of the snout to the orbits. The sinistral spiracle is directed posterodorsally; the spiracular opening is on the midline at midlength of the body. The mouth is anteroventral and has lateral folds bearing one row of papillae; the upper and lower lips are

bare. There are two upper and three lower rows of denticles, of which the second upper row is broadly interrupted medially. The moderately robust beaks are finely serrated. The tail is 60 percent of the total length, is acutely rounded terminally, and has moderately low fins. The dorsal fin barely extends onto the body and is slightly deeper than the caudal musculature or ventral fin. The body and caudal musculature are black with small cream flecks on the tail; the caudal fins are gray. The iris is grayish bronze.

Tadpoles were found in a rocky pool in the riverbed and in temporary ponds in clearings. Feeding aggregations of about 30-50 individuals were observed in shallow (± 10 cm) water in a grassy pool.

Mating Call.—The call consists of a low, rattling trill; in many cases, the call lasted more than 1 min.

Food.—In addition to 7 millipedes (Diplapoda), the stomachs of 25 individuals contained a variety of insects with large ants predominating (68% of stomachs), followed by beetles (Coleoptera, 64%), orthopterans (40%), hemipterans (8%), and lepidopteran larvae (8%).

Remarks.—Throughout its broad geographic range, *Bufo marinus* either avoids, or occurs in low densities, in tropical rainforests. However, it frequently occurs in large populations along river banks and clearings in otherwise forested areas. My observations on the species in Brasil, Colombia, Ecuador, México, and Central America reveal that breeding always occurs in aquatic situations that receive direct sunlight. Perhaps the thermal requirements of the embryos are such that the shaded ponds in forests are unsuitable for embryonic development.

Bufo typhonius (Linnaeus)

(FIGURE 78)

Rana typhonius Linnaeus, 1758, Syst. Nat., 10: 211 [Type locality.—"Americas"].



FIG. 78.—*Bufo typhonius*, ♀, 83 mm SVL (KU 123963).

Bufo typhonius—Schneider, 1799, Hist. Amphib., 1:207.

Material.—Lago Agrio, 9; Puerto Libre, 2; Puerto Ore, 0+3; Santa Cecilia, 244+7.

Identification.—This moderate-sized toad with a pointed snout has an elongate elliptical parotoid gland about one and one-half the length of the eyelid. The dorsum is tuberculate. The cranial crests are high and expanded in adults. A crest extends posteriorly from the snout, angles laterally to the anterior corner of the orbit, and continues posteriorly as a supraorbital and supratympanic crest, ending at the parotoid gland. In large adults the supraorbital crest is expanded dorsally and the supratympanic crest is flared dorsolaterally above the tympanum. A row of pointed tubercles extends from the posterior end of the parotoid gland posteroventrally to the groin. The shape of the parotoid gland, nature of the cranial crests, and the lateral row of tubercles distinguish this species from other *Bufo* in the area. *Bufo glaberrimus* has smooth skin on the dorsum and lacks cranial crests; *B. marinus* has low keratinized cranial crests and lacks a lateral row of pointed tubercles.

The dorsal ground color is tan, gray, or brown, plain or marked with irregular darker blotches and/or pairs of small chocolate brown spots. In most individuals the sides of the head and flanks below the row of tubercles are dark brown.

Many individuals have a middorsal creamy white or yellow middorsal stripe extending from the tip of the snout to the rump. Some individuals have a narrow cream labial stripe. The throat, chest, and anterior part of the belly vary from coppery brown to dark brown; the rest of the venter is yellowish or grayish tan with gray or black flecks. The iris is bronze with a narrow greenish gold border to the pupil. Breeding males have horny nuptial excrescences on the thumbs. ♂ 62 mm; ♀ 87 mm.

Occurrence.—Although this terrestrial toad mostly inhabits primary forest (87% of 232 specimens), 26 were in secondary forest, three in forest-edge situations, and one in a clearing. Adults and juveniles are active on the forest floor by day. Of 66 individuals found at night, 62 were on sticks or leaves up to 1.5 m above the ground; many of these obviously were asleep. Two were on the ground at night, and two were calling from the ground at edges of a stream and the river at night.

Life History.—Gravid females were found throughout the year, except in January, June, and September; however the absence of females from those months evidently is an artifact of sampling. Sixteen gravid females having snout-vent lengths of 58–87 ($\bar{x}=73.3$) mm contained 765–2500 ($\bar{x}=1566.5$) mature ovarian eggs. Two others, having snout-vent lengths of 54 and 61 mm, contained 430 and 310 eggs, respectively. These small ovarian complements may be due to the small size of the females or they may represent only partial ovarian complements. The pigmented eggs are deposited in strings in pools in streams and in temporary pools in the forest. Six metamorphosing young from June have snout-vent lengths of 7.1–8.1 ($\bar{x}=7.6$) mm.

Tadpoles.—Tadpoles in developmental stage 41 have body lengths of 8.5 mm and total lengths of 23.5 mm. The body

is ovoid, widest and deepest at mid-length. The snout is bluntly rounded in dorsal view and round in profile. The eyes are medium-sized, moderately separated, and directed dorsolaterally. The nostrils are midway between the tip of the snout and the orbit. The spiracle is sinistral; its opening is directed postero-dorsally on the midline at midlength of the body. The caudal musculature is slender. The caudal fins are deeper than the musculature and are rounded terminally. The dorsal fin is deeper than the ventral fin and does not extend onto the body. The mouth is anteroventral and has lateral folds bearing one row of papillae. The upper and lower lips are bare. There are two upper and three lower rows of teeth; the second upper row is interrupted medially. The beaks are slender and finely serrate. The body and tail are brown; the fins are translucent.

Mating Call.—The call consists of 3-5 quickly repeated, low-pitched, rattling notes; calls are repeated at intervals of 10-15 seconds. Notes are 0.15-0.20 sec in duration and have a dominant frequency of about 1500 Hz.

Food.—Ants occurred in all 25 stomachs examined; among the 325 ants eaten, many exceeded 17 mm in length. Thirty-five beetles had been eaten by 12 toads. Other food items were represented by single prey and included an isopod, a millipede, a hemipteran, and an orthopteran.

Taxonomic Comments.—Recently it has come to my attention that the toad that is widespread in tropical South America and called *Bufo typhonius* is a composite of perhaps three species. Through the courtesy of Charles W. Myers, I have examined Peruvian specimens in the American Museum of Natural History. Some of the Peruvian females have numerous pigmented eggs, whereas others have few unpigmented eggs. M. S. Hoogmoed (pers. com.) has discerned two morphological types in Surinam, differing in body proportions and the size

and shape of the parotoid glands; both types have pigmented eggs. Ronald Altig (pers. com.) thinks he can distinguish two mating calls and corresponding differences in call sites in these toads in Amazonian Ecuador. I have not subjected the specimens from Santa Cecilia to a detailed morphometric analysis, but all females from Santa Cecilia have numerous pigmented eggs.

***Dendrophryniscus minutus* (Melin)**

(FIGURE 79)

Atelopus minutus Melin, 1941, Göteborgs Vetensk Samh. Handl., 4:18 [Type locality.—Taracúá, Territorio Amazonas, Brasil].

Dendrophryniscus minutus—McDiarmid, 1971, Bull. Los Angeles Co. Mus. Nat. Hist. Sci. 12:40.

Material.—Santa Cecilia, 157.

Identification.—This small toad-like species has a depressed body, pointed snout, and small pointed tubercles on all dorsal surfaces. The absence of parotoid glands and cranial crests distinguish *Dendrophryniscus* from *Bufo*. The venter in *Dendrophryniscus* is purplish red, a character that readily distinguishes the species from two other tubercular toad-like species—*Physalaemus petersi* (black and white venter) and *Ischnocnema quixensis* (cream venter with brown spots).

The dorsum is pale brown, and the flanks are reddish tan; both have minute, pale blue flecks. The throat is grayish brown; the chest, belly, and ventral surfaces of the thighs are purplish red or red with black or brown flecks. A white or pale yellow labial stripe continues onto the anterior surface of the upper arm. The iris is brown peripherally and gold medially. ♂ 16 mm; ♀ 24 mm.

Occurrence.—*Dendrophryniscus minutus* is active on the forest floor by day; individuals take refuge amidst leaf litter. At night they sleep on leaves of low herbaceous plants, usually less than 50 cm above the ground. These shade-loving frogs usually are found only in undisturbed primary forest; only eight



FIG. 79.—*Dendrophryniscus minutus*, ♀, 18 mm SVL (KU 146201).

individuals were found in secondary forest.

Life History.—Gravid females were found throughout the year, except for October. Fifty-two females having snout-vent lengths of 18–22 ($\bar{x}$ = 19.7) mm contained 70–245 ($\bar{x}$ = 162.2) pigmented ovarian eggs. Eggs were not collected at Santa Cecilia; however Duellman and Lynch (1969:238) described eggs resulting from amplexant pairs found at Sarayacu, Provincia Pastaza, Ecuador. The pigmented eggs were in gelatinous strands.

Tadpoles.—The following description is based on tadpoles in stage 31 from Sarayacu, Provincia Pastaza, Ecuador, having body lengths of 5.8 and 6.5 mm and total lengths of 14.1 and 15.4 mm. The body is ovoid, widest posteriorly and slightly wider than deep. The snout is round in dorsal view and in lateral profile. The eyes are moderately large, narrowly separated, and directed dorso-laterally. The nostrils are at a point about 60 percent of the distance from the tip of the snout to the orbits. The sinistral spiracular opening is directed posteriorly on the deadline at about two-thirds the length of the body. The mouth is small and anteroventral with slightly infolded lips that bear a single row of small papillae laterally. The upper and

lower lips are bare. There are two upper and three lower rows of denticles, all complete. The beaks are moderately slender and finely serrated. The tail is about 67 percent of the total length, deepest at midlength, and rounded terminally. The dorsal fin does not extend onto the body, is slightly deeper than the ventral fin and about equal in depth to the caudal musculature at the midlength of the tail. The body and caudal musculature are brown; small black flecks are present on the tail.

Mating Call.—The call consists of two or three quickly repeated, short, high-pitched notes. Analysis of one recording reveals that the duration of each note is about 0.06 sec, and that a sequence of three notes was produced in 0.4 sec. The dominant frequency is about 4200 Hz.

Food.—The stomachs of 25 individuals contained 547 prey items, of which 519 were ants, a prey found in every stomach. Eleven individuals also had eaten 15 small beetles. Other incidental prey included two symphylids, two mites, and one each of the following: beetle larva, homopteran, hymenopteran, millipede, and phalangida.

Remarks.—Most specimens from Santa Cecilia have rather uniform purplish red venters; a few specimens have small creamy yellow spots on the posterior part of the belly. All specimens examined from south of the Río Napo have large yellow or orange spots on the belly.

DENDROBATIDAE

Colostethus marchesianus (Melin)

(PLATE 1)

Phylllobates marchesianus Melin, 1941, Göteborgs Vetensk. Samh. Handl., 4:64 [Type locality.—Taracua, Territorio Amazonas, Brasil].

Colostethus marchesianus—Edwards, 1971, Proc. Biol. Soc. Washington, 84:148.

Material.—Puerto Libre, 2; Santa Cecilia, 93+3.

Identification.—This small frog with

scutes on the dorsal surfaces of the terminal segment of each digit is nearly uniform brown above with black flanks bordered below by a white stripe. It is most easily confused with *Colostethus sauli*, a larger frog with dark brown, usually transverse markings on the dorsum and a diagonal yellow stripe on the flank. Other dendrobatids have black and white or black and blue mottling ventrally.

The dorsum is dull brown usually with a reddish or olive tint; dorsolaterally, the color is paler, giving the indication of an indistinct tan stripe in some individuals. Small dark brown or black flecks are present middorsally in a few specimens. The limbs are pale brown with dark brown transverse markings; in most individuals a pale yellow or yellowish tan spot is evident on the proximal upper surface of the arm. The loreal region and flanks are dark brown or black. The upper lip is cream; a narrow white stripe extends from the angle of the jaw to the groin. A narrow area below the stripe is mottled tan and cream. The belly is creamy white to pale yellow, and the ventral surfaces of the limbs are grayish white. In males the vocal sac is pale yellow. The iris is black with bronze flecks. ♂ 18 mm; ♀ 18 mm.

Occurrence.—*Colostethus marchesianus* is equally abundant in primary and secondary forest, where it is active on the ground by day. Periods of greatest activity are early in the morning or late afternoon, especially after showers. The frogs take shelter in crevices under roots of trees, in stilt palms, or amidst leaf litter. This species is not associated with streams, as are most other species of *Colostethus*; instead individuals are widely dispersed in the forest. Males call from the ground or, more frequently, from slight elevations, such as a stick, large leaf, or base of a tree. At night individuals sleep on leaves of low herbs, usually less than 25 cm above the ground.

Life History.—Gravid females were found in every month except September, December, and January — all months in

which no females were collected. Evidently the species breeds throughout the year. Ovarian complements were 7-27 ($\bar{x}=13.4$, $N=50$). Two males were found carrying tadpoles; one in February had three tadpoles on its back, and one from July had ten.

Tadpoles.—Free swimming tadpoles in stage 30 (KU 109314) have body lengths of 7.7 mm and total lengths of 20.7 mm. The body is ovoid, widest medially, shallower than wide, and deepest posteriorly. The snout is bluntly round in dorsal view and round in profile. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed dorsally at the midline at about three-fifths the length of the body. The mouth is directed anteroventrally and has small lateral folds. The upper lip is bare; elsewhere around the mouth there is a single row of small labial papillae. There are two upper and three lower rows of denticles. The first upper row is on the margin of the upper lip. The second upper row is broadly separated medially. The tail is about 63 percent of the total length. The caudal musculature is robust, its depth at the midlength of the tail being equal to twice the depth of the dorsal fin. The dorsal and ventral fins are about equal in depth, deepest at about midlength of the tail. The dorsal fin does not extend onto the body, and the tip of the tail is round. The body is brown above and below; the tail is cream with brown blotches, and the iris is bronze.

The only free swimming tapoles were found in a water-filled segment of a fallen bamboo in March. One metamorphosing individual having a short tail stub had a snout-vent length of 7.0 mm.

Mating Call.—The call consists of a soft single "peep."

Food.—In 25 stomachs, ants (25) and small beetles (17) were the most abundant prey items, followed by termites

(8). The remaining items (Diptera, Hymenoptera, Orthoptera, and spiders) accounted for only 12 percent of the items and 20 percent of the volume of food eaten.

Colostethus sauli Edwards

(PLATE 1)

Colostethus sauli Edwards, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 30:10 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 3; Santa Cecilia, 19+6.

Identification.—This dull-colored dendrobatid is most easily confused with *Colostethus marchesianus*, a smaller frog with a yellow or white venter and a white ventrolateral stripe and no large dark dorsal markings; *C. sauli* has a gray venter, no white ventrolateral stripe, and dark dorsal marks. Of the other predominately brown dendrobatids in the area, *Dendrobates pictus* has a narrow white canthal and dorsolateral stripe, and *Phylllobates femoralis* has a broad cream canthal and dorsolateral stripe; both have mottled venters.

The dorsum is olive-brown to olive-gray with irregular, but usually transverse, black markings. The limbs are brown with distinct dark brown transverse bars and a pale yellow spot proximally on the upper arm. The side of the head and the flanks are black. A narrow diagonal stripe extends posteroventrally on the flank to the groin; anteriorly the stripe is yellow, changing to bluish gray posteriorly. The anterior and posterior surfaces of the thighs are mottled with shades of gray. The ventral surfaces are uniform pale gray. The iris is grayish bronze. ♂ 22 mm; ♀ 26 mm.

Occurrence.—Unlike the other dendrobatids in the area, this species most frequently occurs near small streams. At two small hillside springs at Santa Cecilia, the frogs were found in shallow water and under overhanging banks. Other individuals were found near the streams issuing from the springs, and a

few were widely dispersed in the forest. Those individuals in the vicinity of streams took refuge in the water, where they would either sit on the bottom or hide beneath submerged objects.

Life History.—Of nine adult females (March 2, May 2, July 4, and August 1), six contained 6-14 ($\bar{x}=11.3$) large ovarian eggs; one from July had small ovarian eggs, and two from July showed no evidence of reproductive activity.

Tadpoles.—Free-swimming tadpoles in stage 36 (KU 109322) have body lengths of 7.8 mm and total lengths of 24.2 mm. The body is elongately elliptical in dorsal view, widest posteriorly, shallower than wide, and deepest posteriorly. The snout is round in dorsal view and in profile. The eyes are large, widely separated, and directed laterally. The nostrils are about 60 percent of the distance from the tip of the snout to the orbits. The opening of the sinistral spiracle is directed posterodorsally on the midline at about three-fifths of the length of the body. The mouth is directed anteroventrally and has small lateral folds. The upper lip is bare; one row of small labial papillae are present laterally and ventrally. There are two upper and three lower rows of denticles, of which the second upper row is widely separated medially. The beaks are slender and finely serrated; the upper beak is deeply notched. The tail is about 68 percent of the total length. The caudal musculature is robust and at midlength of the tail is about thrice the depth of the dorsal fin. The tip of the tail is acutely rounded. The body is black with white flecks, and the tail is black with white mottling.

Tadpoles were found amidst detritus in shallow streams issuing from springs in March and June. One metamorphosing young had a snout-vent length of 7.2 mm.

Mating Call.—The call consists of a series of two or three quickly repeated peeps.

Food.—In eight stomachs, ants (9) and small homopterans (7) were the

only prey items found more than once; other food items were a small beetle (7 mm), beetle larva (11 mm), wasp, and grasshopper nymph. The largest homopterian was 8 mm long.

Dendrobates parvulus Boulenger

(PLATE 1)

Dendrobates parvulus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 145 [Type locality.—Sarayacu, Provincia Pastaza, and Loreto, Provincia Napo, Ecuador].

Material.—Lago Agrio, 15; Puerto Libre, 17; Puerto Ore, 1; Santa Cecilia, 254+1.

Identification.—This small dendrobatid with a red, granular dorsum and a bright yellow spot at the base of each limb cannot be confused with any other frogs in the area. Although other species of *Dendrobates* also have black and blue mottled venters, all have some dorsal stripes and none is red.

The dorsum of the body is a uniform dull red; in some specimens there is a suffusion of gray or dull brown, especially posteriorly. The dorsal surfaces of the limbs are bluish black to dark gray with or without a brownish tint; pale blue or white flecks are evident on the limbs in most individuals. The flanks are blue with black mottling, but in some individuals the black is so extensive as to give the appearance of a black flank with scattered blue spots. The side of the head is black; a narrow bluish white labial stripe usually extends onto the anterior edge of the upper arm. Each individual has a bright yellow spot on the proximal posterodorsal surface of the upper arm and another spot on the proximal anterodorsal surface of the thigh. A bright yellow spot is present on the proximal ventral surface of the shank in most individuals. The throat, belly, and ventral surfaces of the limbs are blue with black spots and mottling. The iris is dark brown to black with minute bronze flecks and a narrow bronze ring around the pupil. ♂ 20 mm; ♀ 23 mm.

Occurrence.—*Dendrobates parvulus* is one of the most abundant and conspicuous frogs living on the forest floor; it is especially abundant (or at least most easily observed) in primary forest. The frogs are most active by day—early in the morning or after afternoon showers; diurnal retreats include the leaf litter, cavities beneath logs, and bases of stilt palms. At night the frogs sleep on leaves of herbs and ferns, usually less than 50 cm above the ground. Males call from sticks, logs, or other slight elevations; usually the calling site is hidden beneath plant cover.

Life History.—Gravid females were found in every month. Of 169 females, only seven (from five scattered months) showed no evidence of reproductive activity, and only 10 (March-June) had only small ovarian eggs. Of the 152 females having large ovarian eggs, 78 were from March-June. The ovarian complement is 4-16 ($\bar{x}=9.0$, $N=152$). Two males carrying five and six tadpoles were found in July.

Tadpoles.—Four back-riding tadpoles have body lengths of 4.0-4.4 ($\bar{x}=4.2$) mm and total lengths of 12.5-13.8 (13.2) mm. The beaks are thin, and no denticles are present. One individual was placed in water and preserved 17 days later; it had better developed beaks, one row of labial papillae laterally and ventrally, and two upper and two lower rows of denticles (second upper row broadly interrupted medially). The body is dark brown, and the tail is tan with dark brown flecks.

Mating Call.—The call of *Dendrobates parvulus* consists of two soft peeps, the second higher pitched than the first.

Food.—Ants were present in each of 23 examined; 120 ants comprised 65 percent of the volume. The remaining prey items were small beetles (14), beetle larvae (2), fly larvae (2), mites (2), and a termite (1). The largest prey item was a fly larva 8 mm long.

Taxonomic Comments.—Silverstone

(1975) placed this species in the genus *Phyllobates* because of the presence of maxillary teeth (see Savage, 1968, for generic definitions). Charles W. Myers (pers. com.) stated that the skin toxins and behavior of *parvulus* definitely ally the species with *Dendrobates*.

Dendrobates pictus pictus

Duméril and Bibron

(PLATE 1)

Dendrobates pictus Duméril and Bibron, 1841, *Erpétol. Gen.*, 8:656 [Type locality.—"Chile"].

Dendrobates pictus pictus—Lutz, 1952, *Mem. Inst. Oswaldo Cruz*, 50:612.

Material.—Lago Agrio, 1; Puerto Libre, 4; Santa Cecilia, 116.

Identification.—This dull greenish gray to dark brown dendrobatid with a black and blue venter can be distinguished from all other dendrobatids and *Lithodytes lineatus* in the area by the presence of a narrow white stripe across the tip of the snout; the stripe continues posteriorly in a dorsolateral position to the groin. *Phyllobates femoralis* and *Lithodytes lineatus* have broader, cream or tan dorsolateral stripes; *P. femoralis* also has white stripe on the flank, and *L. lineatus* has bright red spots on the thighs and pale gray venter. *Dendrobates pictus* lacks a stripe on the flank and red spots on the thighs.

The dorsum is predominately dark brown with a greenish or grayish tint. Scattered, small black spots usually are evident on the back. The limbs are brown with indistinct dark brown cross-bars. A narrow white or creamy white transverse stripe on the snout is continuous with a dorsolateral stripe along the canthus, edge of upper eyelid, and body to the groin. A white labial stripe extends from the lip just anterior to the orbit onto the anterior edge of the upper arm. The side of the head and flanks are black. A small yellow spot is present in the axilla, another on the proximal ventral surface of the shank. The throat,

belly, and ventral surfaces of the limbs are blue, heavily mottled with black. The iris is dull bronze. ♂ 21 mm; ♀ 24 mm.

Occurrence.—Most specimens were found in secondary forest sleeping on leaves of low herbs at night. Others were active by day on the ground in both primary and secondary forest. Eight were sleeping at night on herbs in a marsh adjacent to forest.

Life History.—No individuals were found in January or April; gravid females were found in all other months, except December, in which the only female found showed no evidence of reproductive activity. Such individuals comprise only 13 percent of the females and are from seven months from March through December. Ten percent of the females had only small ovarian eggs; these are from February, June, July, and October. The evidence overwhelmingly indicates that *Dendrobates pictus* breeds throughout the year. The ovarian complement is 10-31 ($\bar{x}$ =18.6, N =53) eggs.

Tadpoles.—Tadpoles were described by Lesure (1976).

Mating Call.—The call is a soft "tick-tick," or "tick-tick-tick."

Food.—Ants were present in all but two of 26 stomachs examined; 110 ants comprised 60 percent of the volume of food. Beetles (16) and termites (6) were the next most common prey items. Other prey items and their frequency of occurrence are: Hemiptera (3), fly larvae (3), Diptera (2), small annelids (2), and one each of the following: Dermaptera, Hymenoptera, coleopteran, larvae, and pseudoscorpion.

Taxonomic Comments.—Silverstone (1975) placed this species in *Phyllobates*; I retain the species in *Dendrobates* pending forthcoming biological definitions of the genera by Charles W. Myers.

Dendrobates quinquevittatus

Steindachner

(PLATE 1)

Dendrobates tinctorius var. *quinquevittatus*

Steindachner, 1864, Verh. Zool.-Bot. Gesell. Wien, 14:260 [Type locality.—"Brasil and Colombia"].

Material.—Lago Agrio, 5.

Identification.—This small dendrobatid has a black dorsum with five broad, bright yellow stripes that readily distinguish it from all other frogs in the area.

The dorsum is jet black. Five broad, longitudinal, bright yellow stripes are arranged as follows: middorsal stripe from top of head to midpoint on body; dorsolateral stripes from snout or canthal region, along edge of eyelid to groin; lateral stripes extending along lip, above insertion of arm, and along the flank to the groin. The middorsal and dorsolateral stripes are variously interconnected by transverse yellow stripes. The dorsal surfaces of the limbs are yellowish tan with black spots. The throat is yellow, and the belly and ventral surfaces of the limbs are blue. All ventral surfaces are marked with large black spots. The iris is dull brown. ♂ 14 mm; ♀ 16 mm.

Occurrence.—All specimens were found in April and May on the ground in primary forest at Lago Agrio. Despite its small size, *Dendrobates quinquevittatus* should have been found at Santa Cecilia. No explanation is evident for the apparent absence of the species at Santa Cecilia.

Life History.—Two females collected in May have 4 and 9 large ovarian eggs. No other data are available.

Tadpoles.—Tadpoles are unknown.

Mating Call.—The call is unknown.

Food.—One individual contained 32 small ants.

Phyllobates femoralis (Boulenger)

(PLATE I)

Prostherapis femoralis Boulenger, 1883, Proc. Zool. Soc. London, 1883:635 [Type locality.—Yurimaguas, Departamento Loreto, Perú].

Phyllobates femoralis—Parker, 1935, Proc. Zool. Soc. London, 1935:506.

Material.—Lago Agrio, 4; Puerto Ore, 1; Santa Cecilia, 44+2.

Identification.—This large dendrobatid has a brown dorsum with cream or tan dorsolateral stripes. The presence of a white stripe on the posterior part of the flank distinguishes *P. femoralis* from all other dendrobatids in the area, except *Colostethus sauli*. The latter species lacks dorsolateral stripes and has a gray venter; the venter is mottled blue and black in *P. femoralis*. Superficially, *P. femoralis* resembles *Dendrobates pictus* and *Lithodytes lineatus*. The former has narrow white dorsolateral stripes and no white stripe on the flank, and the latter has bright red spots on the thighs, no white stripe on the flank, and a gray venter.

The dorsum varies from dark brown or nearly black to olive-brown or reddish brown; in some paler individuals bronze flecks are evident. A dorsolateral stripe extends along the canthus and edge of the eyelid to the groin; the stripe varies from silvery white to cream or tan. A narrow white labial stripe extends along the lip to the base of the arm. A longitudinal bluish white to pale yellow stripe extends from the midflank to the base of the thigh. The side of the head and flanks are black. The forearm is tan with black spots, and the hind limb is mottled reddish tan and black with bluish white flecks. A pale yellow spot is present on the proximal dorsal surface of the arm, and another is present on the proximal anterior surface of the thigh. The throat and chest are black, and the other ventral surfaces are blue heavily mottled with black. The iris is brown. ♂ 25 mm; ♀ 29 mm.

Occurrence.—Individuals were found in equal abundance in primary and secondary forest, where they are active on the ground by day. The frogs are widely dispersed in the forest and not associated with water. Males call from secluded sites early in the morning and late in the afternoon, especially after showers.

Life History.—No females were found in January, February, September, or De-

cember. Gravid females were found in all other months. With the possible exception of the period December-February, breeding evidently occurs throughout the year. The ovarian complement is 8-43 ($\bar{x}=22.4$, $N=15$) eggs. One male was carrying tadpoles in May.

Tadpoles.—One back-riding tadpole (KU 125893) has a body length of 3.6 mm and a tail length of 7.4 mm. There is a single row of labial papillae laterally and ventrally, and two upper and three lower rows of denticles; the second upper row is broadly interrupted medially. The dorsum is pale brown with yellowish tan flecks, and the rest of the tadpole is translucent with brown flecks on the tail.

Mating Call.—The call of this species is a series of high-pitched, quickly repeated pairs of notes: “peep-peep, peep-peep, peep-peep.”

Food.—Twenty-one individuals had eaten a variety of small insects and spiders. Ants were the most common food item retrieved from stomachs, followed by Coleoptera, Hymenoptera, and spiders; five other orders (Lepidoptera, Isoptera, Hemiptera, Diptera, and Orthoptera) also were present. The largest prey taken were beetles; one 8 mm long was eaten by a frog 26 mm in snout-vent length, and one 7 mm long by a frog 27 mm in length.

HYLIDAE

Hemiphractus proboscideus (Jiménez de la Espada)

(FIGURE 80)

Cerathyla proboscidea Jiménez de la Espada, 1870, Jour. Math. Phys. Nat., Lisboa, 3:64 [Type locality.—Sumaco, Provincia Napo, Ecuador].

Hemiphractus proboscideus—Trueb, 1974, Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 29:38.

Material.—Lago Agrio, 1; Puerto Libre, 5; Santa Cecilia, 46.

Identification.—This bizarre frog with a fleshy proboscis, dermal “horns” on the



FIG. 80.—*Hemiphractus proboscideus*, ♀, 58 mm SVL (KU 124139).

eyelids, bony posterolateral projections on the head, and depressed body with protruding neural spines of the vertebrae is entirely unlike any other frog known from the area. Any damn fool should be able to identify this species. *Cerato-phrys cornuta* is the only other species having dermal “horns” on the eyelids, but that species has a robust body and lacks a fleshy proboscis.

In dorsal view, the head is triangular with the posterior margin elevated and concave, the posterolateral corners being formed by three converging body ridges: one posterolaterally from the orbit, one dorsally from the angle of the jaw, and one transversely across the back margin of the skull. Bony canthal ridges diverge from a common point just posterior to the nostrils, extend to the orbits and join the supraorbital ridges, which extend posteromesially to the transverse occipital ridge. A laterally compressed, fleshy proboscis projects from the tip of the snout. A single large dermal tubercle, bordered by several small tubercles, is present on each eyelid. A small triangular calcar is present on the heel. The fingers are not webbed, and the toes are webbed basally. At night the dorsum is yellowish tan with brown transverse or diagonal marks on the body and transverse bars on the limbs; the venter is grayish cream to white. By day the dor-

sum is brown with darker brown markings and the venter is brown to reddish brown with orange or yellowish blotches on the belly and yellow or white spots on the throat. The discs on the first and second fingers are pale orange, changing to white in preservative. The tongue is orange. The iris is pale gray, with a pinkish tint in some individuals, with diffuse darker gray triangular marks anteriorly and posteriorly. ♀ 50 mm; ♂ 67 mm.

Occurrence.—Ecological data are available for 39 specimens, of which 35 were found in primary forest; the others were in secondary forest. One was in leaf litter by day, and the others were perched on low vegetation (usually leaves or palm fronds less than 1.5 m above the ground) at night. Observations on this and other species of *Hemiphractus* (except *scutatus*) indicate that they remain on the forest floor by day, where their coloration and disruptive form provide excellent concealment amidst leaf litter. At night they ascend low vegetation. The presence of both diurnal and nocturnal prey in their stomachs reveals that they feed by day and night. The distribution of specimens from throughout the year is uneven: March (4), April (5), May (4), June (17), July (15), August (5), November (1).

Life History.—Females of this species brood eggs on the back, where they undergo direct development into small frogs. No brooding females were found. In fact only one gravid female was discovered; that individual was found in July, and it contained 26 ovarian eggs 2.5 mm in diameter. Juveniles having snout-vent lengths of 16 mm and 28 mm were found in the same area of forest on 29 March and 15 June 1972, respectively. On 2 April 1972 four juveniles having snout-vent lengths of 18-19 mm were found in an area of about 20m²; on 10 May 1972 another juvenile having a snout-vent length of 23 mm was found

at the same place. These five frogs may be part of one brood.

Mating Call.—Apparently this species does not have a mating call; one male emitted a "grunt" when picked up.

Food.—*Hemiphractus proboscideus* is a carnivore with a prodigious appetite. Ten of 13 stomachs contained 15 frogs, including *Eleutherodactylus croceoguinis* (1), *E. diadematus* (1), *E. lathantites* (2), *E. variabilis* (1), *E. sp.* (1), *Leptodactylus mystaceus* (1), dendrobatid (1), *Hyla fasciata* (1), *H. granosa* (2), *H. sp.* (1), *Osteocephalus lepieurii* (1), and unidentified frog (2). Invertebrate prey included one each: leech, annelid worm, homopteran, and mole cricket (Gryllotalpidae). Some of the prey items were nearly as long as the frogs that had eaten them.

Remarks.—Some individuals, when disturbed, open their cavernous mouths exposing the bright yellow tongue. Subsequent prodding by a careless observer can result in a quick snap of the jaws in a vice-like grip.

In 1967 and 1968 *Hemiphractus* was reasonably abundant at Santa Cecilia. Increasing disturbance of the forest seemed to result in the disappearance of these frogs except in deep primary forest.

Conceivably *Hemiphractus johnsoni* Noble and *H. scutatus* (Spix) occur in the environs of the Río Aguarico. The latter species has a broader head with shorter posterolateral horns and no noticeably expanded discs on the digits; *H. johnsoni* also is more robust than *H. proboscideus* and has a much smaller proboscis (see Trueb, 1974, for diagnoses of the species).

Hyla alboguttata Boulenger

Hyla alboguttata Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 385 [Type locality.—Sarayacu, Provincia Pastaza, Ecuador].

Material.—Santa Cecilia, 153.

Identification.—Although this dull brown *Hyla* could be confused with several other brown frogs in the area, it is distinguishable by several characters.

The absence of webbing between the fingers and/or the absence of fleshy calcars on the heels distinguish *H. alboguttata* from *H. boans*, *calcarata*, *fasciata*, and *geographica*, all of which have dark markings on the flanks and posterior surfaces of the thighs (absent in *H. alboguttata*). *Hyla alboguttata* shares the absence of webbing on the hand and reduced webbing between the first and second toes with *H. cruentomma*, *funerea*, *garbei*, and *rubra*. The latter has yellow spots on the posterior surfaces of the thighs; *H. garbei* has a pointed snout, tubercles on the heels, and vertical black and yellow bars on the posterior surfaces of the thighs. *Hyla cruentomma* and *funerea* have dark brown longitudinal marks on a tan or olive-tan dorsum. Juveniles of *H. alboguttata* and *Osteocephalus lepreurii* have broad, creamy white dorsolateral stripes. The juveniles of *O. lepreurii* have dark transverse bars on the limbs; these are absent in *H. alboguttata*.

The head is broad and flat. Webbing is absent on the hand, and the toes are only about one-half webbed. The skin on the dorsum is smooth; that on the venter is granular. The tympanum is large. The dorsum is tan, usually marked with small, irregular dark brown or black spots; the spots are most numerous mid-dorsally on the posterior half of the body. Dark brown spots are present on the dorsal surfaces of the shanks. The flanks and anterior and posterior surfaces of the thighs are creamy tan. The throat and belly are white with minute, reddish brown flecks, and the ventral surfaces of the limbs are dull brown. The edge of the upper lip is cream. Juveniles (< 25 mm snout-vent length) have broad, creamy white dorsolateral stripes that are narrowest on the head and widest in the scapular region. On the head the stripes are bordered below by dark brown canthal and supratympanic stripes. In specimens 25-30 mm in snout-vent length, the dorsolateral stripes and the dark stripes became diffuse, and

in most specimens having snout-vent lengths of more than 30 mm, there is no evidence of stripes. The iris is greenish gold with bold black reticulations. Breeding males have brown horny nuptial excrescences on the thumbs. ♂ 34 mm; ♀ 46 mm.

Occurrence.—Although *Hyla alboguttata* was found in a wide variety of habitats including clearings, banana groves, swamps, and primary forest, 75 percent of the individuals were in second growth forest, where they were found on low vegetation (< 1.5 m) at night (2% were at heights of more than 1.5 m) throughout the year. Juveniles and subadults were found during the day in unrolling *Heliconia* leaves.

Life History.—Despite the abundance of this species, no breeding or calling were observed. Females with mature ovarian eggs were found in every month, except December. Twenty-one gravid females with snout-vent lengths of 35.0-46.0 ($\bar{X}=41.4$) contained 218-870 ($\bar{X}=440.1$) eggs. The eggs are small (1.4 mm) and pigmented. The smallest juvenile, taken in July, has a snout-vent length of 10 mm.

Tadpoles.—The tadpoles are unknown. On the basis of the number and size of ovarian eggs, it is presumed that *Hyla alboguttata* deposits eggs in standing water.

Mating Call.—The call is unknown.

Food.—Nine arthropod orders were represented in 25 stomachs. Orthopterans were the most common prey (48% of stomachs), followed by dermapterans (24%), beetles (16%), spiders (16%), and lepidopteran larvae (12%). Other prey items were found in less than 10 percent of the stomachs.

Remarks.—Field investigations on this abundant species have been frustrated by the apparent absence of activity by the frogs. Despite the collection of 153 specimens and observations on at least twice that many individuals in the field, no frog was observed to do more than sit on a leaf or branch.

Hyla bifurca Andersson

(PLATE 2)

Hyla (*Hylella*) *bifurca* Andersson, 1945, Ark. Zool. Stockholm, 37A(2):79 [Type locality.—Río Pastaza, Provincia Pastaza, Ecuador].

Hyla bifurca—Duellman, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 27:15.

Material.—Puerto Ore, 31; Santa Cecilia, 96+14.

Identification.—This small brown frog with cream dorsal markings can be confused only with other members of the *Hyla leucophyllata* group, all of which have axillary membranes and external tympana. *Hyla bifurca* is dark brown with the top of the head anterior to the eyes cream; beginning on the eyelids is a pair of parallel, straight-edged, narrow, dorsolateral cream stripes extending posteriorly at least to the sacrum. A small cream spot is present on the rump and on each heel. The dorsal surfaces of the shanks are uniform brown, the flanks, hidden surfaces of the thighs, and webbing on the feet are orange brown. *Hyla bifurca* is most likely to be confused with *H. leucophyllata* and *H. sarayacuensis*, both of which have orange webs and hidden surfaces of the thighs. In *Hyla leucophyllata* the dorsolateral stripes are broad, constricting the middorsal brown area in the scapular region, thereby forming an hour-glass shaped, middorsal dark mark; the dorsal surfaces of the thighs are predominantly tan or cream. The dorsal markings in *H. sarayacuensis* are similar to those in *H. bifurca*, but in the former the dorsolateral stripes are broad, have irregular edges, and extend posterolaterally; furthermore, irregular transverse cream markings are present on the shanks. *Hyla favosa* also has orange flash colors, but the dorsum is dark brown with a network of narrow cream lines. The flash colors are pink or red in *H. triangulum*, and the dorsum is cream to tan with or without one or more dark brown spots.

The snout is broadly rounded in dor-

sal view and truncate in profile. An extensive axillary membrane extends nearly to the elbow. The fingers are webbed basally, and the toes are about two-thirds webbed. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsum is pale brown, with or without minute black flecks; the snout, dorsolateral lines, and spots on the rump and heels are yellowish tan. The hands, feet, axillae, and ventral surfaces of the limbs are orange. Of 111 specimens the rump spot is discrete in 83, connected with one of the dorsolateral lines in 15, and connected with both lines in 13. The vocal sac is yellow; males lack horny nuptial excrescences. The iris is grayish bronze. ♂ 28 mm; ♀ 35 mm.

Occurrence.—No individuals were found in primary forest, but 9 (12%) were found in secondary forest and 11 (14%) in forest-edge habitats. These individuals were perched on leaves or branches of herbs or low bushes; five frogs were on vegetation higher than 1.5 m above the ground. Most of the frogs were found at breeding sites in non-forested areas – temporary ponds or water-filled ditches in clearings or at the edge of a lake. None was found by day.

Life History.—*Hyla bifurca* seems to be an opportunistic breeder. Males call after rains throughout the year, and usually perch on emergent vegetation within 30 cm of the water. Gravid females were found in all months, except June and December through February. Twenty gravid females having snout-vent lengths of 29.0-35.0 ($\bar{X}$ =32.9) mm contained 145-255 ($\bar{X}$ =190.0) eggs. Fifteen clutches contained 153-255 ($\bar{X}$ =191.0) eggs, 2.0 mm in diameter. The heavily pigmented eggs are deposited on the upper surfaces of leaves of emergent plants, usually within 30 cm of the water.

Tadpoles.—The following description is based on tadpoles (KU 146785) in developmental stage 32 having body lengths of 9.5 mm and total lengths of

31.0 mm. In dorsal view, the body is violin shaped with a truncate snout; in lateral view, it is ovoid and deepest posteriorly with an acutely rounded snout. The eyes are large and situated laterally. The nostrils are about midway between the tip of the snout and the orbits. The opening of the sinistral spiracles is directed posterodorsally on the midline at about midlength of the body. The mouth is anterior and lacks lateral folds. The median part of the upper lip is bare; elsewhere there is one row of large, blunt labial papillae. The beaks are moderately robust and finely serrated. Denticles are absent. The tail is about 70 percent of the total length. The fins are moderately deep, the depth of the caudal musculature at midlength of the tail being about 75 percent of the depth of the dorsal fin, which does not extend onto the body. The tail terminates in a long filament. The dorsum of the body is tan with broad black lateral stripes bordered below by a metallic cream stripe. The belly is silvery white with three longitudinal black stripes. The caudal musculature and distal part of the dorsal fin are black; a cream stripe is present on the proximal part of the caudal musculature. The tip of the tail and other fins are cream, with black flecks on the dorsal fin. The iris is reddish bronze.

Tadpoles have been found in shallow, vegetation-choked, temporary pools and ditches. Although individual tadpoles have been observed near the surface in open water, upon being disturbed they seek refuge amidst the vegetation.

Mating Call.—The call consists of a harsh primary note usually followed by two shorter secondary notes. Analysis of nine recordings made at Santa Cecilia revealed that the note repetition rate of primary notes is 15.3-73.2 ($\bar{x}$ =33.9) notes per minute. The duration of the primary notes is 0.06-0.15 ($\bar{x}$ =0.09). The pulse rate is 100-120 ($\bar{x}$ =105) pulses per second. There usually are three harmonics, of which the funda-



FIG. 81.—*Hyla boans*, ♀, 90 mm SVL (KU 109424).

mental at 2625-3339 ($\bar{x}$ =2984) Hz is emphasized.

Food.—Twenty-five adults had eaten a variety of small arthropods. Dipterans (36% of stomachs) were the most common prey, followed by spiders (20%), lepidopterans (12%), and beetles (8%). The largest item of prey was a moth 16 mm long eaten by a frog having a snout-vent length of 25 mm.

Hyla boans (Linnaeus)

(FIGURE 81)

Rana boans Linnaeus, Syst. Nat. 10, Stockholm, p. 213 [Type locality.—“America”].

Hyla boans—Duellman, 1971, Herpetologica, 27:398.

Material.—Santa Cecilia, 123+1.

Identification.—This large brown tree frog has small triangular calcars, extensive webbing on the hands and feet, and pigmented reticulations on the lower eyelid. Furthermore, males have a projecting propollex. *Hyla geographica* is the only other brown tree frog in the area having calcars and reticulations on the eyelid; it differs from the larger *H. boans* in coloration and in the amount of webbing. Webbing extends to about the middle of the outer finger in *H. geographica* but to the base of the disc in *H. boans*. In *H. geographica* the flanks and anterior and posterior surfaces of the thighs are marked by distinct, narrow, dark vertical bars, whereas in *H. boans* vertical bars are present, but they are diffuse on the flanks and barely distin-

guishable on the thighs. All other brown tree frogs, with which *H. boans* might be confused, lack reticulations on the lower eyelid.

The head is broad; a tympanum is present. The toes and all fingers, except the first, are webbed to the bases of the discs. In males there is a curved prepollical spine. A small triangular calcar is present on the heel. The skin on the dorsum is smooth; that on the belly is granular. The dorsal color varies from tan to reddish-brown, grayish brown, or dark brown, usually with slightly darker mottling on the back and transverse bars on the limbs. By day, the dorsal color usually is paler than at night. The flanks are grayish tan with dark brown vertical marks, and the posterior surfaces of the thighs are grayish brown with faint brown vertical marks. The webbing is brown, and the venter is creamy white. The iris is bronze, and the lower eyelid is reticulated with silvery gold. ♂ 118 mm; ♀ 110 mm.

Occurrence.—Although males have been heard calling from trees in primary and secondary forest, all individuals have been found along the Río Aguarico, where they were sitting on the river bank or in bushes or on large cane-like grasses. These large frogs are most active in the drier times of the year. Their calls seldom were heard during rainy periods. Throughout March 1967 one male (presumably the same individual) began calling at dusk (1800-1830 hrs) daily.

Life History.—Normally, the males of this large species construct shallow, basin-like nests (up to 40 cm in diameter) in muddy river banks; water seeps into the basins, from which the males call and in which females deposit eggs on the surface of the water (Duellman, 1973a). Despite some exposed mud flats on the north side of the large island in the Río Aguarico, no nests were found there. However, males were found calling from, and tadpoles living in, natural depressions in the pebble bank of the Río Aguarico. Many small basins remain

filled with water when the level of the river drops. If the presence of calling males along the banks of the river is a true reflection of breeding activity, then breeding in *Hyla boans* is sporadic and associated with drier times of the year—normally August-September and December-February. Gravid females were found in February (1), March (1), July (18), August (10), October (1), and December (1). Twenty-three of these frogs had snout-vents lengths of 80-110 ($\bar{X}$ =99.0) mm and contained 1300-4800 ($\bar{X}$ =3154) mature ovarian eggs. The pigmented eggs had maximum diameters of 2.1 mm.

Tadpoles.—The following description is based on tadpoles (KU 109428) in stage 37 having body lengths of 15 mm and total lengths of 43 mm. The body is broadly ovoid, widest and deepest posteriorly, and ovoid in lateral view. The snout is round. The eyes are large, moderately separated, and directed dorso-laterally. The nostrils are about three-fifths of the distance from the tip of the snout to the orbits. The opening of the sinistral spiracle is directly posterodorsally on the midline at about midlength of the body. The mouth is ventral. The median part of the upper lip is bare, and the lips are folded laterally; a single row of small labial papillae border the mouth laterally and ventrally. The beaks are moderately robust and finely serrate. There are two upper and four lower rows of denticles, of which the second upper row is interrupted medially and the fourth lower row is much shorter than the others. The tail is about 65 percent of the total length and is acutely rounded terminally. The dorsal fin does not extend onto the body, and at its deepest point at about midlength of the tail the depth of the dorsal fin equals the depth of the caudal musculature and twice the depth of the caudal fin. The dorsum is reddish tan with dark olive-brown markings; the belly is white with a golden hue. The tail is cream with reddish brown reticulations. The iris is bronze.

Tadpoles were found in a rocky pool in the riverbed, where they sought refuge under and between stones. The pool was about 1 m in diameter, and the water was no more than 15 cm deep.

Mating Call.—The call consists of a series of short, loud, low-pitched notes, usually produced in groups of three to ten. Analysis of the calls of three individuals from Santa Cecilia revealed that notes were repeated at rates of 21.4–66.7 ($\bar{X}$ = 38.2) notes per minute. The duration of the notes is 0.18–0.27 ($\bar{X}$ = 0.23), and pulses are produced at a rate of 100–140 ($\bar{X}$ = 117) per second. There are at least two harmonics; the fundamental frequency at 435–565 ($\bar{X}$ = 512) Hz is dominant in three of the notes, whereas the second harmonic is dominant in six others.

Food.—Stomachs of 13 adults revealed the presence of orthopterans (85% of stomachs), lepidopteran larvae (15%), and moths (8%). One frog having a snout-vent length of 76 mm had eaten an orthopteran 25 mm long.

Remarks.—This is the only hyliid frog in the area in which males attain a larger size than females. In Panamá *H. boans* is even larger – males to 132 mm and females to 117.5 mm (Duellman, 1970b: 258). Breder (1946:409) reported nest building by males of *H. rosenbergi*, and Lutz (1960:61) reported the habit in *H. faber* and also observed territoriality and aggressive behavior in *H. faber*. All three species are closely related (Duellman, 1970b:246). Thus, it can be assumed that territoriality is common to all three nest-building species and that perhaps selection favors larger size in males. Larger individuals would tend to be more successful in combat than smaller individuals.

Hyla bokermanni Goin

(FIGURE 82)

Hyla bokermanni Goin, 1960, Ann. Mag. Nat. Hist. (13)2:721 [Type locality.—Tarauaca, Territorio do Acre, Brasil]. Duellman and

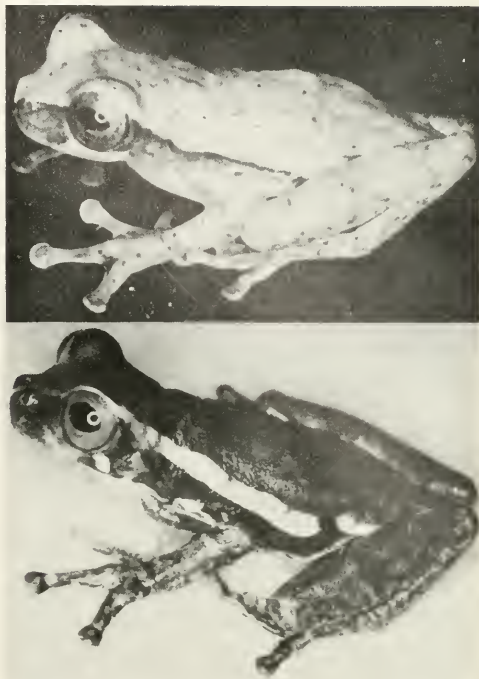


FIG. 82.—*Hyla bokermanni*. Upper: ♂, 23 mm SVL (KU 123089). Lower: ♀, 25 mm SVL (KU 126552).

Crump, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas 23:14.

Material.—Santa Cecilia, 99+12.

Identification.—This small tan frog with a short, truncate snout has dark thighs with yellow spots. Two other small frogs in the area have a pattern of pale spots on dark thighs. *Hyla brevifrons* is like *H. bokermanni* in having one to three small yellow spots on the dorsal surface of the thigh; however, in *H. brevifrons* the anterior surface of the thigh is uniform dark brown, whereas in most specimens of *H. bokermanni* there is a large black-bordered yellow spot on the anterior surface of the thigh. *Hyla parviceps* has dark brown thighs with two small cream spots on the anterior surfaces. Furthermore, *H. parviceps* has a bright orange spot on the proximal ventral surface of the shank (unmarked in *H. bokermanni*) and one vertical cream bar on the upper lip (two bars in *H.*

bokermanni). Other small yellowish tan or brown frogs in the area do not have one to three yellow spots on dark brown thighs.

The snout is short and truncate in dorsal view and profile. The tympanic ring is visible ventrally. An axillary membrane extends about one-half the length of the upper arm. The fingers are about one-third, and the toes about one-half webbed. Breeding males lack nuptial excrescences. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsum is pale yellowish tan; dorsal markings and dorsolateral stripes are barely discernable. By day the dorsum is tan usually with dark markings consisting of many small flecks, three transverse bars, or a large blotch anteriorly and a transverse bar posteriorly. The shanks and forearms are tan with distinct brown crossbars. The thighs are dark brown with two creamy yellow spots on the dorsal surfaces; in 80 percent of the specimens there is a large, oval bright yellow spot, usually with a narrow black border on the anterior surface of the thigh. There are two pale creamy yellow vertical or diagonal bars below the eye. In about half of the specimens a narrow creamy yellow, vertical rostral stripe is present; usually in these specimens the rostral stripe is confluent with a narrow canthal stripe. In males a narrow creamy yellow dorsolateral stripe extends from the outer edge of the eyelid to the mid-upper flank; a short stripe is present in the groin. In females a broad, creamy white stripe and inguinal spot are present. The venter is creamy white, except for a yellow vocal sac in males. The iris is silvery gray with a narrow red ring around the pupil. ♂ 24 mm; ♀ 28 mm.

Occurrence.—About 75 percent of the *Hyla bokermanni* were found in secondary forest; the others were in primary forest. All were found at night on vegetation; only four of 101 individuals were more than 1.5 m above the ground. Males usually call from emergent vegetation in

swamps in, or, less frequently, at the edge of, forest. Most calling males are 1-1.5 m above the water. The frogs were found throughout the year, except December.

Life History.—Gravid females were found in January (1), February (17), March (29), April (29), May (9), June (2), October (1), and November (5). *Hyla bokermanni* seems to be an opportunistic breeder, reaching peaks of reproductive activity at times of heavy rainfall. Duellman and Crump (1974: 23) noted that a *Heliconia*-choked swamp in secondary forest there were peaks of breeding activity in October-November 1971 and in February-April 1972. These were times of greatest water depth in the swamp. During breeding peaks 300-500 males and 10-50 females were estimated to be in the swamp on any given night. Twenty-nine females having snout-vent lengths of 22.5-25.5 ($\bar{X}$ =23.9) mm contained 65-135 ($\bar{X}$ =98.3) mature ovarian eggs. *Hyla bokermanni* deposited eggs on vegetation over the water. The small, lightly pigmented eggs are 1.5-1.8 ($\bar{X}$ =1.6, N =53) mm in diameter. Clutches contained 60-196 ($\bar{X}$ =116.8, N =53) eggs. The eggs require 4.0-5.3 ($\bar{X}$ =4.4, N =20) days to hatch, at which time the hatchlings drop into the water. Hatchling tadpoles have total lengths of 4.0-4.5, ($\bar{X}$ =4.2, N =20) mm. Two recently metamorphosed young have snout-vent lengths of 11.3 and 11.8 mm.

Tadpoles.—The following description is based on tadpoles (KU 124193) in stage 35 having a body length of 6.8 mm and a total length of 18.8 mm (see Duellman and Crump, 1974:13 for illustration). The body is ovoid, widest medially and deepest posteriorly, with a round snout. The eyes are large, widely separated, and directed laterally. The nostrils are about midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is just below the midline at about three-fifths of the length of the body. The mouth is

anterior and lacks lateral folds. The upper lip is bare; one row of labial papillae border the mouth laterally and ventrally. The beaks are moderately robust and finely serrated. Denticles are absent. The tail is about 64 percent of the total length and terminates in a short filament. The tail is deepest at midlength, where the caudal musculature and dorsal fin are of equal depth, but the ventral fin is about 60 percent as deep as the dorsal fin, which does not extend onto the body. The body is dark brown with two short, broad, longitudinal yellowish tan bars on the snout. Proximally, the tail is pale orange; distally, the tail is unpigmented, except for broad gray vertical marks. The iris is silver with a red tint medially.

The tadpoles are pelagic in swamps; they seek cover amidst vegetation or by diving towards the bottom.

Mating Call.—The call consists of a high-pitched primary note followed by two to five shorter secondary notes. Analysis of recordings of four individuals at Santa Cecilia revealed a note repetition rate (primaries) of 5-19 ($\bar{X}=12.2$) notes per minute having durations of 0.23-0.28 ($\bar{X}=0.259$) sec and 100-190 ($\bar{X}=132.5$) pulses per second. The dominant frequency is at about 4500 Hz.

Food.—Sixteen stomachs contained a variety of small arthropods. Ants and orthopterans were each represented in 50 percent of the stomachs; dipterans and lepidopteran larvae were each present in 19 percent of the stomachs. Single prey items were a beetle, beetle larva, homopteran, and spider. These small frogs are capable of taking large prey relative to their body size. One frog having a snout-vent length of 22 mm contained an orthopteran 15 mm in length, and three individuals 18, 23, and 25 mm in snout-vent length contained caterpillars 17, 23, and 15 mm in length.

Remarks.—As noted by Duellman and Crump (1974:22), the three species in the *Hyla parviceps* group (*H. bokermanni*, *brevifrons*, and *parviceps*) at Santa Cecilia are segregated ecologically.

Hyla parviceps is a habitat generalist and breeds sympatrically and synchronously with the other two species, which only rarely were found together. Furthermore, *H. parviceps* deposits eggs in water, whereas the others deposit eggs on vegetation over water.

Hyla brevifrons Duellman and Crump

(FIGURE 83)

Hyla brevifrons Duellman and Crump, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas 23:15 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 3; Puerto Libre, 3; Santa Cecilia, 153+5.

Identification.—This small tan frog with a short, truncate snout has one to three small yellow spots on the otherwise dark brown thighs. Two other frogs in the area have pale spots on dark thighs. *Hyla bokermanni* also has yellow spots on the dorsal surfaces, but most specimens also have a large black-bordered yellow spot on the anterior surface of the thigh. *Hyla parviceps* has two cream spots on the anterior surface of the thigh, a bright orange spot on the proximal ventral surface of each shank (unmarked in *H. brevifrons*), and one vertical cream bar on the upper lip (two in *H. brevifrons*). Other small yellowish tan or brown frogs in the area lack pale spots on the thighs.

The snout is short and truncate in dorsal view and profile. A tympanic ring is visible ventrally. An axillary membrane extends one-half the length of the upper arm. The fingers are about one-half, and the feet about two-thirds, webbed. Breeding males do not have nuptial excrescences. The skin is smooth on the dorsum and granular on the belly. At night the dorsum is pale tan with faintly darker dorsal markings. By day the dorsum is olive-tan with three or four broad transverse brown marks on the back and transverse bars on the forearms and shanks. The thighs are dark brown with 1-3 creamy yellow spots on the dorsal surfaces. Two creamy yellow

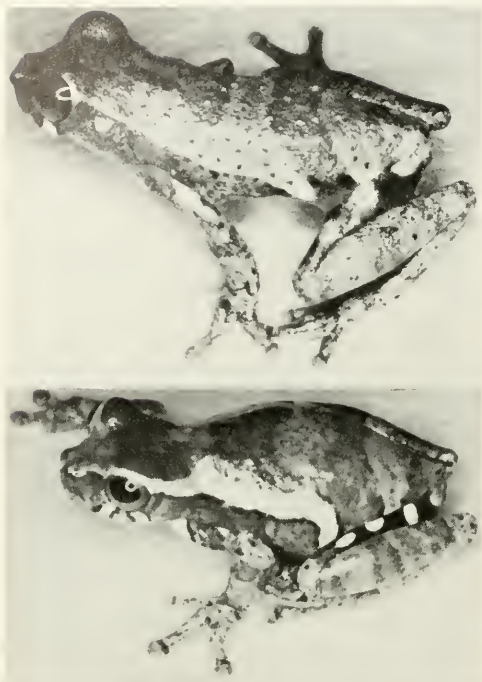


FIG. 83.—*Hyla brevifrons*. Upper: ♂, 19 mm SVL (KU 126370). Lower: ♀, 23 mm SVL (KU 126371).

vertical or diagonal suborbital bars are invariably present; a narrow vertical rostral stripe is present in about half of the specimens, and a narrow cream canthal line is present in about two-thirds of the specimens. In most males and in all females a creamy yellow dorsolateral stripe extends from the outer edge of the eyelid to the midflank region and then ventrally on the flank. The stripe is a very narrow line in males and a distinct broad stripe in females. The chin and chest are white in females, and the vocal sac is yellow in males; other ventral surfaces are unpigmented. The iris is silvery gray with a narrow red ring around the pupil. ♂ 22 mm; ♀ 25 mm.

Occurrence.—All individuals were in secondary forest. Thirteen were perched on low (< 1.5 m) vegetation in the forest, and 121 were on vegetation in and around swamps at the forest edge or, less frequently, in forest. All were found at

night. Individuals were found throughout the year, except in February.

Life History.—Gravid females were found in January (1), March (4), April (1), June (1), July (3), October (2), November (1), and December (2). *Hyla brevifrons* seems to be an opportunistic breeder with peaks of breeding activity correlated with heavy rains. Fifteen females having snout-vent lengths of 18.0–23.5 ($\bar{X}$ = 20.9) mm contained 48–114 ($\bar{X}$ = 79.1) mature ovarian eggs. The small (1.2–1.6, $\bar{X}$ = 1.3 mm; N = 6) lightly pigmented eggs are deposited on vegetation over water. One clutch required 6.3 days to hatch, at which time the tadpoles dropped into the water. A hatchling tadpole had a total length of 6.0 mm. Two recently metamorphosed young had snout-vent lengths of 7.6 and 8.4 mm.

Tadpoles.—The following description is based on a tadpole (KU 125899) in stage 37 having a body length of 7.2 mm and a total length of 23.0 mm (see Duellman and Crump, 1974:13, for illustration). The body is ovoid, widest anteriorly and deepest posteriorly, with a rounded snout. The eyes are large, widely separated, and directed dorsolaterally. The nostrils are about midway between the tip of the snout and the eyes. The opening of the sinistral spiracle is directed posterodorsally just below the midline at about three-fifths of the length of the body. The mouth is anterior and lacks lateral folds; the upper lip is bare, but a row of small labial papillae are present laterally and ventrally. The beaks are moderately robust and finely serrated; denticles are absent. The tail is about 68 percent of the total length and terminates in a short filament. The tail is deepest at about two-thirds of its length, where the ventral fin is nearly as deep as the dorsal fin, and the caudal musculature is about two-thirds of the depth of the dorsal fin, which does not extend onto the body. The body is dark brown with an indistinct, diffuse, tan dorsolateral stripe and cream flecks laterally. The tail is tan with dark brown mottling and

a bright red streak on the dorsal fin. The iris is grayish bronze with a red ring around the pupil.

Tadpoles were found in deep water (± 1 m) in forest ponds, where they took refuge amidst detritus on the bottom.

Mating Call.—The call consists of a series of short insect-like chirps repeated at a rate of 26-46 ($\bar{X}=36.8$, $N=9$) notes per minute. Further analysis of recordings of nine individuals at Santa Cecilia reveals that notes have a duration of 0.43-0.49 ($\bar{X}=0.467$) sec and 30-40 ($\bar{X}=38.9$) pulses per second. The dominant frequency is at about 4600 Hz.

Food.—In 25 stomachs, small beetles (44% of stomachs) were the most common prey, followed by lepidopteran larvae (20%), homopterans and spiders (16% each), orthopterans (8%), and one fly and one ant (4% each). The largest prey item was a caterpillar 17 mm long in a frog 18 mm in length.

Hyla calcarata Troschel

(FIGURE 84)

Hyla calcarata Troschel, 1848 Amphibien, in M. R. Schomburgk, Reisen Britisch-Guiana, 3:60 [Type locality.—Guyana]. Duellman, 1973, Copeia, 1973(3):552.

Material.—Puerto Ore, 12; Santa Cecilia, 96+5.

Identification.—This brown tree frog has large elongately triangular calcars, pale flanks and hidden surfaces of the thighs with bold black markings, no reticulations on the lower eyelids, and no webbing between the fingers. The absence of reticulations on the lower eyelid and webbing between the fingers distinguish *H. calcarata* from *H. boans* and *H. geographica*; the latter has the fingers half webbed, and *H. boans* has nearly fully webbed fingers. Both species have golden reticulations on the lower eyelid. *Hyla calcarata* is most easily confused with *H. fasciata*. In the latter the calcars are smaller and proportionately broader, the black markings on the flanks and



FIG. 84.—*Hyla calcarata*, ♂, 37 mm SVL (KU 111677).

thighs usually are irregular spots, and brown flecks are present on the throat and chest. *Hyla calcarata* has large, elongate calcars, the black markings on the flanks and thighs usually in the form of vertical bars, and an immaculate venter. Two other hylids in the area have calcars and vertical dark marks on the thighs; *Hyla garbei* has broad black and orange bars on the thighs, small conical calcars, a pointed tuberculate snout, and a mottled green, tan, and black dorsum. *Phyllomedusa tomopterna* has bright orange thighs with brown bars, large triangular calcars, no webbing between the toes, and a uniformly green dorsum.

The head is broad; a tympanum is present. Webbing is absent or vestigial between the fingers; the toes are one-half to two-thirds webbed. Breeding males have horny nuptial excrescences on the thumbs. Large, elongate, triangular calcars are present on the heels. The skin on the dorsum is smooth; that on the venter is granular. At night the dorsum is pale yellowish tan with faint darker markings; by day the dorsum is pale reddish brown with brown markings. The dorsal markings consist of: 1) five to seven broad transverse marks, interconnected or not; 2) narrow transverse lines in the interspaces between the broad marks in some individuals; 3) narrow dark brown middorsal line from the tip

of the snout to a point between the occiput and rump; 4) transverse bars on the limbs (one or two each on upper arm and forearm and three to five each on thigh, shank, and foot). The webbing on the foot is brown. The posterior half of the flanks and the anterior and posterior surfaces of the thighs are bluish white in small adults and blue in large adults, usually with vertical black bars about equal in width to the interspaces; in a few individuals the dark markings are in the form of irregular spots. As many as eight vertical bars may be present on the flank or thigh. Narrow creamy white stripes are present above the anus and on the outer edge of the foot. The venter is white; in large females there is a tan suffusion along the margin of the chin. The coloration of juveniles is noticeably different (see Remarks). The iris is creamy silver. ♂ 41 mm; ♀ 61 mm.

Occurrence.—*Hyla calcarata* inhabits forests. All individuals were found on vegetation; most were on branches of bushes less than 1.5 m above the ground. Of 92 individuals with adequate ecological data, 23 were in a forest swamp, 32 were at the edge of a lake, and 5 were along streams in the forest; the others were scattered in the forest away from water. The frogs were observed every month of the year, except December.

Life History.—Although males were heard calling throughout most of the year, only ten gravid females were found—March (3), April (2), August (1), September (1), October (2), November (1). Breeding seems to be associated sporadically with rains throughout the year. The ten females had snout-vent lengths of 47-61 ($\bar{X}$ =53.9) mm and contained 835-1600 ($\bar{X}$ =1143) mature ovarian eggs. Three females having snout-vent lengths of 52.5-57.0 ($\bar{X}$ =55.0) mm deposited clutches of 1060-1250 ($\bar{X}$ =1153) eggs in the laboratory. The pigmented eggs (2.0 mm in diameter) were deposited as a film on the surface of the water. The eggs hatched in 79-86 hrs;

hatchling tadpoles had total lengths of 5.5-7.0 ($\bar{X}$ =6.0) mm.

Tadpoles.—Tadpoles (KU 152292) in developmental stage 33 have body lengths of 9.5 and total lengths of 32.5 mm. The body is ovoid, widest and deepest at midlength, with an acutely rounded snout. The eyes are large, closely set, and directed dorsolaterally. The nostrils are about three-fifths of the distance from the tip of the snout to the orbits. The spiracular tube is long, and the opening of the spiracle is directed posteriorly on the midline at about two-thirds the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare; elsewhere the mouth is bordered by one row of small labial papillae. The beaks are slender with moderate-sized serrations. There are two upper (second interrupted medially) and three lower rows of denticles. The tail is about 72 percent of the total length, and it terminates in a pointed tip. The dorsal fin does not extend onto the body and is deepest at the midlength of the tail, where it is equal in depth to the caudal musculature and half again as deep as the ventral fin. The dorsum of the body is dark brown with faint tan mottling and tan interorbital bar. The tail is yellowish tan with vertical brown bars.

Tadpoles were found in swamps and small sluggish streams in forest.

Mating Call.—The call consists of one or more soft, low-pitched, poorly modulated, monophasic notes. Analysis of one recording from Santa Cecilia revealed a repetition rate of 8 notes per minute. The notes were 0.07 sec in duration and were produced with a pulse rate of 180 pulses per second. The dominant frequency was at about 1400 Hz.

Food.—Twenty-five individuals contained the remains of a diversity of small arthropods and one small frog. Orthopterans were the most common prey (40% of the stomachs), followed by spiders (24%), beetles (8%), homopterans (8%),

lepidopteran larvae (8%), and five other groups each in fewer than 5 percent of the stomachs.

Remarks.—Juveniles having snout-vent lengths of less than 25 mm lack transverse markings on the dorsum and vertical black bars on the flanks and thighs. A faintly darker brown middorsal stripe has five or six lateral expansions, which may be incipient transverse marks.

Hyla cruentomma Duellman

(FIGURE 85)

Hyla cruentomma Duellman, 1972, Copeia 1972 (2):266 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 2; Santa Cecilia, 118+13.

Identification.—This is one of three species of moderate-sized tree frogs in the area having a yellowish tan to greenish tan dorsum with darker longitudinal markings. Among these species, *H. cruentomma* is distinctive in having a silvery bronze iris with a median horizontal red streak. *Hyla cruentomma* is like *H. rubra* in having smooth skin on the dorsum, but *H. rubra* differs by having bold black or dark brown reticulations enclosing yellow spots in the groin and on the posterior surfaces of the thighs. These surfaces are uniform pale green in *H. cruentomma* and yellow or pale green with brown spots or streaks in *H. funerea*, a species having small tubercles on the dorsum and a greenish bronze iris with black flecks.

The snout is round in dorsal view and in profile; an external tympanum is present. Webbing is absent between the fingers; the toes are about one-half webbed, but the webbing is vestigial between the first and second toes. Nuptial excrescences are absent in breeding males. The skin on the dorsum is smooth and that on the belly is granular. The dorsum is yellow, tan, or pale green usually with dark brown markings, most



FIG. 85.—*Hyla cruentomma*, ♂, 27 mm SVL (KU 111924).

often consisting of a canthal stripe, inter-orbital bar, transverse bars on the forearms and shanks, and irregular longitudinal marks on the body. The groin and anterior and posterior surfaces of the thighs are uniform pale green or yellowish green. The ventral surfaces are white in females and pale yellow in males, which have bright yellow vocal sacs. The iris is silvery bronze with a median horizontal red streak. The bones are green. ♂ 28 mm; ♀ 32 mm.

Occurrence.—Most individuals were found in low (< 1.5 m) vegetation in and around temporary ponds; about equal numbers were found in ponds in clearings and in a *Heliconia*-choked pond in secondary forest. All of these frogs were members of breeding congregations. Otherwise, the frogs were on low vegetation in primary forest (13), secondary forest (21), forest edge (2), and banana grove (1). The frogs were found throughout the year, but only eight were collected between August and March.

Life History.—*Hyla cruentomma* seems to be an opportunistic breeder, reaching peaks of reproductive activity after heavy rains. Males usually call head down on leaves or blades of grass covered by other leaves or blades, above water. They call from secluded sites, and are extremely wary; at the slightest disturbance they cease calling and take refuge in dense vegetation. Gravid females were found in February through July; non-gravid females also were found in January, August, and December.

Eighteen gravid females having snout-vent lengths of 25.0-32.0 ($\bar{X}$ =28.3) mm contained 280-1200 ($\bar{X}$ =580) mature ovarian eggs having diameters about 1.1 mm. Five females deposited eggs in the laboratory. The clutches, laid as a film on the surface of the water, contained 590-1200 ($\bar{X}$ =884) eggs with a maximum diameter (ova) of 1.5 mm. The eggs required about 38 hrs to hatch, and hatchlings had total lengths of 3.5-4.0 ($\bar{X}$ =3.8) mm. Four recently metamorphosed young have snout-vent lengths of 11.2-12.2 ($\bar{X}$ =11.7) mm.

Tadpoles.—The following description is based on a tadpole (KU 125932) in stage 30 having a body length of 8.8 mm and a total length of 28.2 mm. The body is ovoid, widest at the level of the eyes and deepest posteriorly. In dorsal view the snout is broadly rounded, in lateral view inclined and truncate terminally. The eyes are large, widely separated, and directed anterolaterally; the nostrils are midway between the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally just below the midline at about two-thirds of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare, and there are two rows of labial papillae ventrolaterally; the rest of the lips are bordered by one row of papillae. The beaks are moderately robust and bear fine, pointed serrations. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially. The tail comprises about 70 percent of the total length and is pointed terminally. The tail is deepest at midlength where the caudal musculature is equal to about 65 percent, and the ventral fin equal to about 90 percent, of the depth of the dorsal fin, which extends onto the body. The body is olive-green with a brown streak from the snout to the orbit; the venter is white with a silvery sheen. The caudal musculature is pale yellow, and the fins are transparent, both with

brown flecks, which becomes a fine network in larger individuals. The iris is bronze with a red horizontal streak.

Tadpoles were found in shallow grassy ponds, where they swim just below the surface. When disturbed they seek refuge amidst aquatic vegetation.

Mating Call.—The call consists of a single, moderately long, soft note. Analysis of one recording made at Santa Cecilia reveals a repetition rate of 4 notes per minute. The notes have a duration of 0.35-0.37 sec and 160-170 pulses per second. The dominant frequency is at about 3300 Hz.

Food.—Food was found in 23 stomachs. Dipterans were found in 26 percent of the stomachs, roaches (22%), spiders (17%), caterpillars (13%), beetles (13%), and homopterans, hemipterans, hymenopterans, and lepidopterans (4% each).

Remarks.—Of the three species in the *Hyla rubra* group (*H. cruentomma*, *funerea*, and *rubra*) at Santa Cecilia, *H. cruentomma* has the most overlap of habitat with the others. *Hyla funerea* is almost exclusively an inhabitant of forest, and *H. rubra* is seldom found in the forest, whereas *H. cruentomma* occurs in both forest and clearings. Both *H. cruentomma* and *H. rubra* call synchronously from the same ponds, and both *H. cruentomma* and *H. funerea* have been found around the same ponds in forest.

Duellman (1972a) described and illustrated the tadpoles and variation in coloration of adult *H. cruentomma*.

Hyla fasciata Günther

(FIGURE 86)

Hyla fasciata Günther, 1859, Cat. Batr. Sal. Brit. Mus.: 100 [Type locality.—"Andes of Ecuador"]. Duellman, 1973, Copeia, 1973 (3):523.

Material.—Durenó, 1; Lago Agrio, 2; Santa Cecilia, 152.

Identification.—This tan *Hyla* has small triangular calcears, pale flanks and



FIG. 86.—*Hyla fasciata*, ♀, 48 mm SVL (KU 122682).

hidden surfaces of the thighs with irregular black spots, no reticulations on the lower eyelids, and no webbing between the fingers. The last two characters distinguish *H. fasciata* from *H. boans* and *H. geographica*, both of which have calcars and golden reticulations on the lower eyelids. *Hyla geographica* has fingers about one-half webbed, whereas the toes are nearly fully webbed in *H. boans*. *Hyla fasciata* is most easily confused with *H. calcarata*, a species having large elongately triangular calcars, vertical black bars on the flanks and thighs, and an immaculate venter; brown flecks are present on the throat and chest in *H. fasciata*. Two other tree frogs in the area have calcars: *Hyla garbei* has small conical calcars, broad black and orange bars on the thighs, a pointed tuberculate snout, and a mottled green, tan, and black dorsum. *Phyllomedusa tomopterna* has bright orange thighs with brown bars, large triangular calcars, no webbing between the toes, and a uniformly green dorsum.

The head is broad; a tympanum is present. Webbing is absent or vestigial between the fingers, and the toes are about one-half webbed. Breeding males have horny nuptial excrescences on the thumbs. Small triangular calcars are present on the heels of most of the frogs, but in some individuals the calcar is conical. The skin on the dorsum is

smooth; that on the belly is granular. The dorsum is yellowish tan with pale brown markings consisting of: 1) narrow mid-dorsal line; 2) four or five broad, irregular marks on the back; 3) narrower diagonal bars on the limbs (one on upper arm, two or three on forearm, four or five on each shank and thigh, and two or three on each foot). The webbing is tan. A faint creamy white stripe usually is evident on the outer edge of the foot. The flanks and anterior and posterior surfaces of the thighs are grayish white (pale blue in large females) with irregular black spots, which are fragmented into dorsal and ventral components in some individuals. The venter is yellowish white with small brown flecks on the throat and chest, and in large females laterally on the belly. The iris is creamy silver. ♂ 37 mm; ♀ 51 mm.

Occurrence.—This species is a forest inhabitant, although far more individuals (75) were found in secondary forest than in primary forest (3). With the exception of one individual on the forest floor, one on a tree trunk, and four on branches more than 1.5 m above the ground, all of the frogs were on low vegetation (< 1.5 m). About 90 percent of these were on branches; the others, on leaves. Calling males were found in a forest swamp. Two males were on bushes in a marsh; three were at the edge of a lake, and eight were along streams in the forest. The frogs have been observed throughout the year.

Life History.—Apparently this species breeds throughout the year. The supporting evidence is the presence of gravid females in every month, except November. Males were only heard on three occasions, always at the same pond. Twenty-seven females having snout-vent lengths of 45–51 ($\bar{X}=47.3$) mm contained 360–870 pigmented ovarian eggs having diameters of 1.5 mm. Presumably this species, like its apparent closest relative (*H. calcarata*), deposits eggs in a surface film in forest ponds.

Tadpoles.—The tadpoles are un-

known. Probably they are pond dwellers with two upper and three lower rows of denticles, like those of *H. calcarata*.

Mating Call.—The call is a soft, low pitched, poorly modulated, diphasic note, repeated at intervals of about 12 sec. Analysis of one recording made at Santa Cecilia revealed that each note is 0.12-0.16 ($\bar{X}=0.145$) sec in duration and has 140-180 ($\bar{X}=164$) pulses per second. The dominant frequency is between 1700 and 1800 Hz.

Food.—Among the diversity of small arthropods found in 23 stomachs, flies (27% of the stomachs) were the most common, followed by roaches (22%), spiders (17%), beetles (13%), caterpillars (13%), and four other orders, each comprising less than 5 percent.

Remarks.—Despite its abundance, our data on *Hyla fasciata* are remarkably incomplete. Males are known to call from only one swamp, yet adults have been found throughout the study area. On the basis of external morphology, osteology, and mating call, *Hyla fasciata* is closely related to *H. calcarata*; thus, it may be presumed that the reproductive behavior of the two are similar. Males of both species have been found calling synchronously in the same swamp. The call differences (duration, phase, and pulse rate) apparently are of sufficient magnitude so as to act as effective isolating mechanisms.

Hyla favosa Cope

(PLATE 2)

Hyla favosa Cope, Proc. Amer. Philos. Soc., 23:95 [Type locality.—Pebas, Departamento Loreto, Perú]. Duellman, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 27:17.

Material.—Santa Cecilia, 10.

Identification.—The distinctive giraffe-like dorsal color pattern immediately distinguishes this species from all others in the area, except for one of the color morphs of *H. triangulum*. In the latter the dorsum is creamy tan with many dark brown spots leaving narrow pale inter-

spaces, and the webbing and hidden surfaces of the thighs are pink or red. In *H. favosa* the dorsal surfaces of the head, body, shanks, feet, and arms and the flanks and the side of the head are dark brown with narrow, creamy white lines forming a fine network; the webbing and hidden surfaces of the thighs are orange. Other species having orange flash colors (*H. bifurca*, *leucophyllata*, and *sarayacuensis*) have dark brown dorsums with pale dorsolateral markings.

The snout is round in dorsal view and in profile. An axillary membrane extends about half the length of the upper arm. The fingers are about half webbed and the toes about two-thirds webbed. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsal surfaces of the head, body, and limbs, and the sides of the head and the flanks are tan with narrow creamy yellow lines forming a network over the entire dorsal and lateral surfaces. The webbing, axilla, anterior and posterior surfaces of the thighs, and ventral surfaces of the limbs are pale orange. The belly is cream. By day the dorsum is dark brown with creamy white lines, and the flash colors are bright orange. The vocal sac is yellow; breeding males lack nuptial excrescences. The iris is orange-bronze. ♂ 36 mm; ♀ 40 mm.

Occurrence.—Ecological data are available on only seven of the ten specimens. Five males were perched on low bushes or saw-grass in a forest-edge swamp in May, and one male was on a bush in the same swamp in March. A female was on a large-leafed herb about 2 m above water in a swamp in a clearing in April. All were found at night.

Life History.—The single gravid female having a snout-vent length of 40.0 mm was found in April. She contained 496 ovarian eggs. Presumably *Hyla favosa*, like other species in the *Hyla leucophyllata* group, deposits eggs on vegetation above water.

Tadpoles.—The tadpoles are unknown. It is presumed that they are like

those of other species in the *Hyla leuco-phyllata* group in having a terminal mouth lacking denticles and a xiphicercal tail.

Mating Call.—The call is unknown. Probably it consists of a primary note and a series of shorter secondary notes.

Hyla funerea (Cope)

(FIGURE 87)

Scytotis funereus Cope, 1874, Proc. Acad. Nat. Sci. Philadelphia 25:123 [Type locality.—Moyobamba, Departamento San Martín, Perú].

Hyla funerea—Duellman, 1971, Herpetologica 27:218.

Material.—Santa Cecilia, 82+4.

Identification.—Of the three species of frogs at Santa Cecilia having yellow, tan, or pale green dorsal ground color with irregular dark longitudinal markings, *H. funerea* is the only one having small tubercles dorsally. The dorsal skin in the other two species (*H. cruentomma* and *rubra*) is smooth. Furthermore, the groin and hidden surfaces of the thighs are yellow or pale green with brown spots or streaks in *H. funerea*, whereas they are uniform pale green in *H. cruentomma* and reticulated with brown or black enclosing yellow spots in *H. rubra*. In *H. cruentomma* the iris is silvery bronze with a median horizontal red streak, whereas in *H. funerea* the iris is greenish bronze with black flecks.

The snout is acutely rounded in dorsal view and in profile, and protrudes beyond the margin of the lip. A tympanum is present. Webbing is absent between the fingers, and the toes are about one-half webbed, except that webbing is vestigial between the first and second toes. Nuptial excrescences are absent in breeding males. The skin on the dorsum is smooth except for scattered low tubercles on the head, body, shanks, and forearms. The skin on the venter is granular. The dorsum is pale green to greenish tan with olive-brown to dark brown markings consisting of : 1) flecks on all dorsal surfaces except upper arms



FIG. 87.—*Hyla funerea*, ♀, 36 mm SVL (KU 146298).

and shanks; 2) interorbital bar; 3) pair of elongate marks in scapular region (interconnected in six individuals); 4) pair of elongate marks in sacral region (interconnected to two individuals); 5) broad canthal stripes narrowly separated medially on snout; 6) bold spots on upper lips; and 7) three transverse bars each on thigh, shank, and tarsus. The flanks and the posterior surfaces of the thighs are yellow with one or two irregular, longitudinal brown stripes or series of dashes on the flanks and dark brown spot and/or a longitudinal bar on the thighs. The ventral surfaces are uniformly creamy yellow except for small brown flecks on the margin of the chin in some males, all of which have bright yellow vocal sacs. The iris is greenish bronze with brown flecks. The limb bones are green. ♂ 36 mm; ♀ 43 mm.

Occurrence.—Most individuals were found in forest (17 primary, 34 secondary); others were in forest edge (2), banana grove (1), and clearing (1). Three individuals were on the ground, and one was on a log; 52 were on vegetation, but only six of these were at heights of more than 1.5 m. All were found at night. Most individuals were found in March through September; only five were found in October through February, and none was found in November or December.

Life History.—Although adult females were found throughout the year,

except November and December, only 13 females having mature ovarian eggs were found – four each in March and April, and one each in January, February, May, July, and September. A call was not associated with this species until late in the field studies, when males were heard calling from trees near a pond in primary forest in September and October. The meager data suggest that *H. funerea* is a sporadic breeder and that possibly it reaches two peaks of breeding coinciding with the rainiest times of the year in April-May and October-November. Thirteen females having snout-vent lengths of 33.0-43.0 ($\bar{X}$ =37.9) mm contained 225-740 ($\bar{X}$ =538) pigmented ovarian eggs about 1.1 mm in diameter. Presumably, like other members in the *Hyla rubra* group, the eggs are deposited as a surface film in temporary ponds. Two recently metamorphosed young obtained on 10 June 1968 have snout-vent lengths of 11.2 and 12.0 mm.

Tadpoles.—The following description is based on tadpoles (KU 152559) in stage 27 having body lengths of 9.5 mm and total lengths of 25.0 mm. In dorsal view the body is ovoid, widest anteriorly, and with a bluntly rounded snout. In lateral view the body is trianguloid, deepest posteriorly, with a round snout. The eyes are large and lateral; the nostrils are at about 60 percent of the distance from the snout to the orbits. The opening of the sinistral spiracle is directed posterodorsally just below the midline about two-thirds of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare; elsewhere there is a single row of labial papillae. The beaks are robust and moderately serrated. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially. The tail is about 62 percent of the total length and is pointed terminally. The greatest depth of the tail is at two-fifths of its length, where the depth of the

caudal fin is slightly less than, and the depth of the caudal musculature is one-half, the depth of the dorsal fin, which extends onto the body. The body is pale green dorsally and laterally and silver ventrally. The tail is pale orange with brown flecks, and the iris is silvery bronze. Larger tadpoles (stage 36) are more yellowish green on the body and tail with brown flecks on the tail, and the iris is bronze.

Tadpoles were found in a pond in primary forest by day and in a pond at the edge of the forest at night.

Mating Call.—The call consists of a moderately long, rather high-pitched, single note. No recordings were obtained.

Food.—Orthopterans, which were found in 64 percent of 25 stomachs containing food, were the most common prey items, followed by lepidopteran larvae (16%), beetles (16%), spiders (12%), and homopterans, dermapterans, dipterans, and dipteran larvae (4% each). Caterpillars 35 and 27 mm long had been eaten by frogs having snout-vent lengths of 41 and 38 mm. The latter also contained a roach 14 mm long, and another individual having a snout-vent length of 31 mm had eaten an orthopteran 17 mm long.

Remarks.—See the account of *Hyla cruentomma* for a discussion of the ecological distribution of *H. funerea* with respect to other members of the *Hyla rubra* group. The variation in, and distribution of, *Hyla funerea* were discussed by Duellman (1971).

Hyla garbei (Miranda-Ribeiro)

(FIGURE 88)

Caribaea garbei Miranda-Ribeiro, 1926, Arch. Mus. Nac. Rio de Janeiro, 27:96 [Type locality.—Eirimepé, Rio Juruá, Território do Amazonas, Brasil].

Hyla garbei—Duellman, 1970, Copeia, no. 3:536.

Material.—Puerto Libre, 2; Puerto Ore, 1; Santa Cecilia, 82+16.

Identification.—This distinctive small



FIG. 88.—*Hyla garbei*, ♂, 37 mm SVL (KU 111680).

hylid is readily distinguished from all other frogs in the area by the following combination of characters: 1) long, acuminate, projecting snout; 2) long slender fingers lacking webbing and bearing truncate discs; 3) elongate tubercle on heel; 4) row of tubercles along edge of lower jaw; and 5) groin and hidden surfaces of thighs yellow or orange with broad black vertical bars. The general appearance of *Hyla garbei* is suggestive of *Eleutherodactylus* more than *Hyla*; however, the combination of characters given above distinguishes *H. garbei* from *Eleutherodactylus*, as well as other *Hyla*.

The snout is long, acuminate, projecting, and usually bearing at least one terminal tubercle. A tympanum is present. The fingers are long and slender, bearing broad, truncate discs; webbing is absent between the fingers, and breeding males lack nuptial excrecences. The toes are about one-half webbed, except that webbing is vestigial between the first and second toes. The skin is smooth above the tubercles on the snout, eyelids, supratympanic fold, heels, and along the outer edges of the forearms and feet. The skin on the throat is smooth and that on the belly granular. The dorsum is pale dull green or reddish brown with dark brown or black markings always consisting of a triangle on the head with the corners on the eyelids and the apex posteriorly. Other dorsal markings usually consist of: 1) supratympanic stripe; 2) indistinct bars on lips, weakly defined

transverse bars on the limbs; 3) large, ovoid marks posterodorsal to the axillae; and 4) small dashes or transverse marks posteriorly on the dorsum. The anterior and posterior surfaces of the thighs are yellow or pale orange with broad black or dark brown vertical bars, usually three on each surface. The venter is creamy white with gray flecks on the chin and, in some individuals, laterally on the belly. The iris is pale creamy bronze with a median horizontal reddish brown streak. ♂ 37 mm; ♀ 48 mm.

Occurrence.—*Hyla garbei* is widespread and abundant at Santa Cecilia, but only one individual was found in primary forest. Others were about equally distributed between clearings and secondary forest, but most of those in secondary forest were at breeding ponds. One individual was on the ground in a clearing; all others were on low (< 1.5) vegetation. All of the frogs were found at night. Individuals were found throughout the year, except in November and January; this probably is an artifact of sampling.

Life History.—*Hyla garbei* probably breeds continuously throughout the year. Males call head down from secluded sites over (usually within 1 m) of water. Calling sites usually are leaves or stems covered by other vegetation. Gravid females have been found in every month except January and November. Twenty-one females having snout-vent lengths of 39.0-48.0 ($\bar{X}$ =41.9) mm contained 280-793 ($\bar{X}$ =551) pigmented ovarian eggs about 1.5 mm in diameter. Eighteen individuals having snout-vent lengths of 37.0-45.0 ($\bar{X}$ =41.3) mm deposited clutches of 445-905 ($\bar{X}$ =727) eggs as a film on the surface of the water. The eggs hatched in 55 to 79 hrs; hatchlings had total lengths of 4.5-5.5 (5.0) mm. Three metamorphosing young had snout-vent lengths of 11.5-12.3 ($\bar{X}$ =11.8) mm.

Tadpoles.—The following description is based on tadpoles (KU 152293) in stage 36 having body lengths of 9.0 mm and total lengths of 29.0 mm. In dorsal

view the body is ovoid, widest anteriorly, with a bluntly round snout; in profile the body is trianguloid, deepest posteriorly, with a round snout. The eyes are large and lateral; the nostrils are about midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally below the midline at about three-fourths of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare; elsewhere, except midventrally, the mouth is bordered by a single row of small labial papillae. The beaks are robust with moderate serrations. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially, and the third lower row is short and protrudes beyond the labial margin. The tail comprises about 70 percent of the total length and terminates in a point. The tail is deep, deepest at about two-fifths of its length, where the dorsal and ventral fins are equal in depth. The depth of the caudal musculature is about 60 percent of the depth of the dorsal fin, which extends onto the body. The body is pale yellowish green above and laterally, and silvery white ventrally. The tail is pale yellowish green with olive-green transverse marks on the caudal musculature and red flecks on the dorsal fin and posterior part of the tail. The iris is bronze with a median horizontal reddish brown streak.

The tadpoles were found in March through August in a variety of temporary and ephemeral ponds, ditches, and swamps. The tadpoles seldom are seen in open water; usually they are in the midst of dense vegetation.

Mating Call.—The call of *Hyla garbei* consists of a single, moderately long note "vraaak." Analysis of recordings of eight individuals from Santa Cecilia reveals that notes are produced at a rate of about 14 per minute; that duration is 0.16–0.26 ($\bar{X}$ = 0.21) sec, and there are 195–240 ($\bar{X}$ = 215) pulses per second. The dominant frequency is at about 3250 Hz.

Food.—In 23 stomachs, orthopterans were the most common prey (70% of the stomachs), followed by spiders (30%) and dipterans and beetle larvae (4% each).

Remarks.—With increased clearing of the forest at Santa Cecilia, *Hyla garbei* seems to have become more abundant. At small ponds in clearings and at the edge of the forest where males called infrequently in 1967 and 1968 they were calling in abundance in 1971 and 1972.

The variation in this species was treated in detail by Duellman (1970a), and the relationships with other members of the *Hyla rostrata* group were discussed by Duellman (1972b).

Hyla geographica Spix

(FIGURE 89)

Hyla geographica Spix, 1824, *Animalia nova. . . testudinum et ranarum. . . Brasiliam*, p. 39 [Type locality.—Rio Tefe, Territorio do Amazonas, Brasil]. Duellman, 1973, *Copeia*, (3):526.

Material.—Durenó, 1; Lago Agrio, 2; Puerto Ore, 1; Santa Cecilia, 89+7.

Identification.—This large brown tree frog has small triangular calcei and pigmented reticulations on the lower eyelid. *Hyla boans* is the only other brown tree frog having calcei and reticulated eyelids; it differs from *H. geographica* in coloration, amount of webbing, and by having prepollical spines in males. Webbing extends to about the middle of the outer finger in *H. geographica*, but to the base of the disc in *H. boans*. In *H. geographica* the flanks and anterior and posterior surfaces of the thighs are marked by distinct, narrow, dark vertical bars, whereas in *H. boans* vertical bars are diffuse on the flanks and barely distinguishable on the thighs. All other brown tree frogs, with which *H. geographica* might be confused, lack reticulations on the lower eyelid.

The head is broad; a tympanum is present. The toes are about three-fourths webbed, and the fingers are about half webbed. Breeding males have horny



FIG. 89.—*Hyla geographicalis*, ♀, 66 mm SVL (KU 111686).

nuptial excrescences on the thumbs. A small triangular calcar is present on the heel. The skin on the dorsum is smooth; that on the belly is granular. The dorsal surfaces of the head, body, and limbs usually are dull tan or brown with faintly darker markings that most frequently consist of an X-shaped mark in the scapular region, irregular transverse marks on the back, and transverse bars on the limbs. A narrow, dark-brown middorsal line is present in many individuals; in some of these the line is evident only on the head, whereas in others it extends to varying lengths on the body. Considerable individual variation obtains in dorsal coloration, and usually the color is paler at night than by day. The variation in dorsal pattern includes: 1) tan with black flecks, 2) uniform yellowish tan, 3) metallic greenish gold with dark brown markings, 4) tan mottled with creamy white. The heels usually are colored like the rest of the body, but in some individuals the heels are white, creamy yellow, or orange. The flanks are creamy to pale gray, and the anterior and posterior surfaces of the thighs are creamy tan to gray, both with narrow vertical dark gray to black bars; those on the flanks, and less frequently on the thighs, are arranged in pairs. In males the venter is creamy white, becoming creamy yellow laterally and posteriorly; in large females the throat and chest are creamy yellow, and the belly and ventral surfaces of the limbs are pale orange. In some individuals the ventral color is pres-

ent on the margin of the upper lip. (The foregoing description applies only to adults; see *Remarks* for comments on ontogenetic variation.) The iris is cream to grayish tan, with or without a red or orange wash; the lower eyelid has golden reticulations. ♂ 62 mm; ♀ 83 mm.

Occurrence.—All individuals of this large tree frog were in forest. Most were found in secondary forest and associated bodies of water. Two individuals were found on the ground by day and when primary forest was being cleared at Lago Agrio. Presumably they were dislodged from arboreal perches when trees were felled. Six others were observed at heights of 1.5-4 m in trees, and all others were on low vegetation (< 1.5 m). Although adults were observed in and near ponds and swamps in the forest, breeding congregations were found only at the edge of a lake. Males called from dense bushes usually within 0.5 m of the ground and within 2 m of the edge of the lake. The frogs were observed throughout the year, except December and January.

Life History.—*Hyla geographicalis* breeds sporadically throughout the year, usually following heavy rains. Gravid females were found in March (1), June (2), July (11), August (5), September (3), October (1), and November (2). Seven of these having snout-vent lengths of 64.5-69.0 ($\bar{X}$ =66.6) mm contained 1780-4300 ($\bar{X}$ =2797) mature ovarian eggs. In the laboratory, one female deposited 2434 pigmented eggs 2.0 mm in diameter as a film on the surface of the water. The eggs failed to hatch. Metamorphosing young found in the field had snout-vent lengths of 20.5 and 22.5 mm.

Tadpoles.—Tadpoles (KU 146789) in developmental stage 33 have body lengths of 20 mm and total lengths of 52 mm. The body is ovoid, widest at mid-length and deepest posteriorly. The snout in dorsal view is bluntly round, and in profile, round. The eyes are small, widely separated, and directed dorsolat-

erally. The nostrils are midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally on the midline about three-fifths of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare, whereas one row of small labial papillae is present laterally and ventrally. The beaks are slender with fine serrations. There are two upper (second interrupted medially) and four lower rows of denticles. The tail is about 62 percent of the total length and is acutely rounded terminally. The dorsal fin does not extend onto the body and is deepest at midlength of the tail, where its depth equals that of the caudal muscular and greatly exceeds that of the ventral fin. The body and caudal musculature are black; the caudal fins are opaque gray.

Tadpoles have been found only in water up to 1.5 m in depth near the shore of the lake. Although no attempt was made to collect tadpoles in deeper water farther from shore, no schools were observed while personnel were working gill nets in deep water. They occur in large schools, perhaps exceeding 1000 individuals, and at least sometimes are just below the surface. Due to the depth and murkiness of the water, no observations could be made on the schooling behavior.

Mating Call.—The call of this species varies from a series of short chuckles to a long groan. Of four individuals recorded at Santa Cecilia, one produced only long notes, one only short notes, and two both. The short notes have a duration of 0.04-0.09 ($\bar{X}$ =0.06) of a second and have 170-190 ($\bar{X}$ =183) pulses per second. The dominant frequency is at 140-1950 ($\bar{X}$ =1710) Hz. The long notes have a duration of 0.13-0.30 ($\bar{X}$ =0.213) sec and have 80-160 ($\bar{X}$ =131) pulses per second. The dominant frequency is at 100-1400 ($\bar{X}$ =1208) Hz.

Food.—Twenty-one orthopterans were found in 18 (72%) of 25 stomachs

examined. The only other food items occurring in more than one stomach were beetles (24%) and spiders (8%). Six other kinds of food (moth, caterpillar, ant, dermapteran, isopteran, and phalangid) were present, each in one stomach. Adults of *Hyla geographica* consume moderately large items of prey. In the following list the lengths of the prey is given after the name, and the snout-vent length of the frog in parentheses: orthopteran – 26 mm (62 mm), orthopteran – 30 mm (64 mm), beetle – 24 mm (61 mm), caterpillar – 36 mm (40 mm).

Remarks.—Ontogenetic change in coloration is striking in *Hyla geographica*. Recently metamorphosed young have a creamy tan dorsum with many black flecks on the head, body, and dorsal surfaces of the limbs. The venter is pale gray; the flanks, anterior and posterior surfaces of the thighs, and the inner surfaces of the shanks are black. As the frogs increase in size, the black spots on the dorsum are replaced by brown markings, and the black pigment on the flanks and limbs concentrates to form a pattern of vertical bars. This ontogenetic change was documented by Hennessy (1968) and discussed by Duellman (1973b).

Hyla geographica is the only anuran at Santa Cecilia known to breed only in a lake. There the tadpoles are potentially subject to predation by many kinds of fish; for example, the cichlid *Crenichichla lepidotus* and the characins *Hoplias malabaricus*, *Leporinus friderici*, *Serrasalmus nattereri*, and *Triportheus elongatus*, have been found in the lake. Possibly the schooling behavior of the tadpoles acts to reduce predation.

Hyla granosa Boulenger

(FIGURE 90)

Hyla granosa Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 358 [Type locality.—Canelos, Ecuador; Santarém, Brasil; and Demerara Falls, Guyana].

Material.—Dureno, 1; Lago Agrio, 1; Santa Cecilia, 53+6.



FIG. 90.—*Hyla granosa*, ♀, 42 mm SVL (KU 122736).

Identification.—This moderate-sized, primarily green *Hyla* is most easily confused with *Hyla punctata*, a green frog with red flecks and a red dorsolateral stripe, bordered above by a yellowish white dorsolateral stripe. *Hyla granosa* lacks dorsolateral stripes and usually is uniform green dorsally, although some individuals have a reddish brown or black canthal stripe, interorbital bar, or small spots on the back. Furthermore, in *H. granosa* the outer finger is about one-third webbed, the skin on the dorsum is finely granular, and males have projecting prepollical spines. In *H. punctata* the outer finger is only basally webbed, the dorsal skin is smooth, and males lack projecting prepollical spines. The species of *Sphaenorhynchus* differ from *H. granosa* by having much more webbing on the hand and by having acuminate, protruding snouts. The one bright green *Eleutherodactylus* (*E. acuminatus*) lacks webbing on the hands and feet, lacks an external tympanum, and has a pointed snout and truncate discs, whereas *H. granosa* has a tympanum and round discs. The species of *Centrolenella* all have truncate discs and gold, yellow, or white flecks on a green dorsum, and *Phyllomedusa* lack webbing on the feet.

The snout is broadly rounded in dorsal view and round in profile. An external tympanum is present. The outer finger is about one-third webbed, and the second and third fingers are basally

webbed; the toes are about two-thirds webbed. Breeding males lack horny nuptial excrescences, but adult males have projecting prepollical spines. The skin on the dorsum is finely granular; that on the belly is coarsely granular. In most individuals the dorsum is uniform pale green. In some individuals minute red flecks are visible on the dorsum. In about five percent of the specimens, there are reddish brown or black dorsal markings that maximally consist of a canthal stripe, interorbital bar, two to four spots on the sacral region, or transverse bars on the shanks. The groin and hidden surfaces of the limbs are green, with a bluish tint in some individuals. The venter is nearly transparent but has a faint greenish tint. The fingers and toes are greenish yellow, and the edge of the upper eyelid is cream. The vocal sac is green, and the iris is pale cream. ♂ 54 mm; ♀ 44 mm.

Occurrence.—Only two individuals were found in clearings. All others were in primary or secondary forest. All frogs were on vegetation at night. Males commonly were heard after rains throughout the year along the forested shores of the lake and in two forest-edge swamps. No individuals were found in November through January.

Life History.—*Hyla granosa* breeds sporadically at times of heavy rainfall. Gravid females were found in February (1), March (2), April (3), June (2), July (2), and August (1). Eleven females having snout-vent lengths of 40.0–44.0 ($\bar{X}=41.2$) mm contained 350–520 ($\bar{X}=426$) pigmented eggs. Presumably, these are deposited as a surface film on the water. The smallest, recently metamorphosed young has a snout-vent length of 14.2 mm.

Tadpoles.—The following description is based on tadpoles (KU 125902) in stage 25 having body lengths of 7.5 mm and total lengths of 22.5 mm. The body is ovoid, wider than deep, and widest anteriorly. The snout is broadly rounded in dorsal view and round in profile. The

eyes are large, narrowly separated, and directed dorsolaterally; the nostrils are midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally below the midline at about the mid-length of the body. The mouth is antero-ventral and has lateral folds. The median part of the upper lip is bare; elsewhere one row of small labial papillae border the mouth. The beaks are slender with fine serrations. The single upper row of denticles is narrowly interrupted medially; the two lower rows are complete. The tail comprises about 67 percent of the total length and terminates in a point. The fins are shallow; the tail is deepest at midlength, where the depth of the caudal musculature is equal to the depth of the dorsal fin, and where the depth of the ventral fin is about two-thirds of the depth of the dorsal fin, which does not extend onto the body. The body and caudal musculature are dull, pale green, and the fins are transparent.

Tadpoles were obtained from amidst aquatic vegetation in swamps at the edge of the forest.

Mating Call.—The call consists of a series of two to four notes, “boop-boop-boop.” Analysis of ten recordings made at Santa Cecilia reveals that the call rate is 14-40 ($\bar{X}=24.7$) notes per minute and that the notes are produced at a rate of 40-80 ($\bar{X}=57.8$) per minute. Notes are 0.03-0.18 ($\bar{X}=0.078$) sec in duration and have 240-400 ($\bar{X}=299$) pulses per second. The dominant frequency is at 1217-1587 ($\bar{X}=1390$) Hz.

Food.—Eight stomachs contained four beetles, two moths, three orthopterans, and two spiders.

Hyla lanciformis (Cope)

(FIGURE 91)

Hyssibous lanciformis Cope, 1870, Proc. Amer. Philos. Soc., 11:556 [Type locality.—Pebas, Departamento Loreto, Perú].

Hyla lanciformis—Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 361.



FIG. 91.—*Hyla lanciformis*. Upper: ♂, 80 mm SVL (KU 122778). Lower: juvenile, 19 mm SVL (KU 122739).

Material.—Puerto Libre, 1; Puerto Ore, 2; Santa Cecilia, 176+19.

Identification.—Adults of this large tree frog are easily distinguished from all other frogs in the area by the following combination of characters: 1) snout long and pointed; 2) creamy yellow labial and supra-anal stripes; 3) throat and chest brown with large cream spots; 4) fingers basally webbed; 5) males having projecting prepollical spine. *Leptodactylus mystaceus* also has a cream labial stripe, but it has a uniform white or yellow venter and no prepollical spines. Juveniles (< 25 mm snout-vent length) are yellowish tan with longitudinal brown lines on the dorsum. The presence of a white supra-anal stripe and a brown median stripe and brown dashes on the throat distinguish them from other juvenile hylids having similar dorsal patterns (*Hyla alboguttata*, *H. calcarata*, *H. fasciata*, and *Osteocephalus lepieurii*).

The snout is long and pointed in dorsal view and round in profile. The promi-

ment tympanum is nearly as large as the eye. The outer fingers are webbed basally, and the inner fingers lack webbing; the toes are about two-thirds webbed. Males lack horny nuptial excrescences but have a projecting prepollex. The skin on the dorsum is smooth; that on the belly is granular. At night the dorsum is tan; by day it changes to brown or olive-tan. Dorsal markings consist of six to eight transverse brown or olive-brown bars on the dorsum of the body. Usually the anteriormost bar is between the eyes. A distinct creamy yellow to silvery white labial stripe extends from the tip of the snout to the angle of the jaw. The side of the head is olive-green to dark brown. The anterior and posterior surfaces of the thighs are tan to pale olive-green. A transverse creamy yellow to silvery white stripe is present above the anus, and similarly colored narrow stripes are present on the heels. The throat, chest, and ventral surfaces of the limbs are brown; large cream spots are present on the chest. The belly is cream, with a suffusion of gray in some individuals. The dorsal surfaces of the discs on the first three fingers are creamy white. The iris is bronze. ♂ 80 mm; ♀ 94 mm.

Occurrence.—*Hyla lanciformis* is an abundant frog, active throughout the year. Although the frogs are most abundant in clearings, where they are active on the ground, they are most readily observed in second growth forest, where many individuals perch at night on branches or stems of low (< 1.5 m) bushes and trees. Observations at Muñozlandia suggest that these frogs seek diurnal refuges beneath fallen palm fronds and other debris and in clumps of grass.

Life History.—This species apparently breeds continuously throughout the year. Males call every night of the year; calling sites usually are branches or trunks of low trees and bushes in, or adjacent to, shallow, temporary ponds in clearings or at the edge of the forest. Gravid females were obtained in every

month, except January, June, and December. Twenty-three females having snout-vent lengths of 79.0-94.0 ($\bar{X}=87.3$) mm contained 740-2400 ($\bar{X}=1617$) eggs having diameters of 2.0 mm. Three clutches of 2100-2400 ($\bar{X}=2250$) pigmented eggs, 2.0 mm in diameter, were deposited as a surface film on the water and hatched in about 80 hrs into tadpoles 6.0 mm long. The smallest metamorphosed young had a snout-vent length of 13.9 mm.

Tadpoles.—The following description is based on tadpoles (KU 112332) in stage 35 having body lengths of 14 mm and total lengths of 45 mm. The body is ovoid, wider than deep, widest and deepest medially. The snout is round in dorsal view and in profile. The eyes are large, widely separated, and directed dorsolaterally. The nostrils are about midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posteriorly just below the midline at a point about three-fourths of the length of the body. The mouth is anteroventral and has lateral folds. The upper lip is bare; elsewhere the mouth is bordered by one row of small labial papillae. The beaks are slender and bear moderate-sized serrations. There are two upper and three lower rows of denticles. The second upper row is interrupted medially, and the third lower row is much shorter than the others. The tail is about 70 percent of the total length and terminates in a point. The fins are shallow. The tail is deepest at midlength, where the depth of the ventral fin equals about 60 percent, and the depth of the caudal musculature equals the depth of the dorsal fin, which does not extend onto the body. The body is dark brown above and laterally, and gray ventrally, with green lichenous markings. The caudal musculature is tan, and the fins are transparent, both marked with vertical dark brown bars. The iris is dull reddish brown.

Tadpoles were found in nearly every kind of temporary aquatic environment

in clearings and at the edge of the forest.

Mating Call.—The call consists of a loud chuckle-like note. Analysis of four recordings made at Santa Cecilia reveals that notes are produced at a rate of 9.1–18.8 ($\bar{X}=13.0$) per minute. The notes are 0.22–0.39 ($\bar{X}=0.275$) sec in duration and have 160–220 ($\bar{X}=200$) pulses per second. The dominant frequency is the second harmonic at 660–728 ($\bar{X}=697$) Hz.

Food.—Examination of 20 stomachs revealed orthopterans (60% of the stomachs) to be the most common prey, followed by beetles (10%), homopterans (10%), and dermapterans, lepidopterans, dipteran larvae, pedipalps, and spiders (5% each). For its size, *Hyla lanciformis* does not eat large prey. Except for one grasshopper 45 mm long eaten by a frog having a snout-vent length of 78 mm, the largest prey items were 17 and 19 mm.

Remarks.—On several occasions, *Hyla lanciformis* were observed to be captured in Muñozlandia by day by foraging domestic chickens, and two were captured by diurnal snakes (*Chironius*). When grasped by a snake or chicken, the frogs emit a loud distress call. When captured, females frequently emit a distress call, but males seldom do.

Hyla leucophyllata (Bercis)

(PLATE 2)

Rana leucophyllata Bercis, 1783, Sber. Gesell. Naturf. Fr. Berlin, 1783:182 [Type locality.—Surinam].

Hyla leucophyllata—Gravenhorst, 1829, Delic. Mus. Zool. Vratislav., Batr., p. 31. Duellman, 1974, Oecas. Pap. Mus. Nat. Hist. Univ. Kansas, 27:18.

Material.—Santa Cecilia, 81+7.

Identification.—This distinctive species can be confused only with *H. bifurca* and *H. sarayacuensis*, all of which have orange webbing and hidden surfaces of the thighs, although the orange is heavily suffused with brown in some *H. bifurca*. In all three species the top of the head anterior to the eyes is cream to tan; a

pair of pale marks extends posteriorly from the eyelids. These marks have irregular edges and extend posterolaterally in *H. sarayacuensis*, whereas they have smooth edges and are parallel, extending posteriorly in *H. bifurca* and *H. leucophyllata*. The marks are narrow in *H. bifurca*, in which the dorsal surfaces of the shanks are uniformly dark brown, and a small cream or tan spot is present on the rump and on each heel. The marks are broad in *H. leucophyllata* and delineate a dark brown, middorsal hour-glass-shaped mark; the dorsal surfaces of the shanks are predominantly pale. *Hyla favosa*, which also has orange flash colors, has a dark brown dorsum with a network of creamy white lines. The morphologically similar *Hyla triangulum* has pink or red flash colors and a uniformly pale dorsum or one or more small dark spots.

The snout is broadly rounded in dorsal view and truncate in profile. An axillary membrane extends to about the midlength of the upper arm. The fingers are about half webbed and the toes about two-thirds webbed. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsum is yellowish tan with brown markings consisting of a large hour-glass-shaped middorsal mark extending from the eyelids to the sacrum and a border around the head and body. Thus, the tip of the snout, sides of the head, and flanks are brown. The supra-anal region, dorsal surfaces of the thighs and arms, and outer surfaces of the shanks are brown. In some individuals the posterolateral corners of the middorsal mark are connected with the dark flanks. In other specimens one or two narrow brown transverse bars are present on the dorsal surfaces of the shanks, which otherwise are yellowish tan. By day, the dorsum is creamy tan to white with dark brown markings. The venter is cream. At night the hands, feet, axillae, anterior and posterior surfaces of the thighs, and ventral surfaces of the limbs are yellowish

orange; by day these surfaces are orange. The vocal sac is yellow; males lack nuptial excrescences. The iris is dull bronze. ♂ 36 mm; ♀ 44 mm.

Occurrence.—Only three individuals were found on vegetation at night in secondary forest; none was found in primary forest. Most individuals were found on bushes and emergent grasses in a permanent forest-edge swamp, and others were in a *Heliconia* swamp and a temporary forest-edge swamp.

Life History.—*Hyla leucophyllata* breeds sporadically after heavy rains, at which time males call from bushes around, and herbs or grass emerging from, forest-edge ponds. With the exception of September, gravid females have been found in April through October. Twelve females having snout-vent lengths of 40.0-44.0 ($\bar{X}$ =42.1) mm contained 220-928 ($\bar{X}$ =572.3) eggs. Three clutches contained 570-769 ($\bar{X}$ =669.7) eggs, 1.5 mm in diameter. The lightly pigmented eggs are deposited on the upper surfaces of leaves of emergent vegetation, usually less than 50 cm above the water.

Tadpoles.—The following description is based on tadpoles (KU 112337) in stage 36 having body lengths of about 8.0 mm and total lengths of 28.0 mm. In dorsal view, the body is violin-shaped with a round snout; in lateral view, shallowly ovoid, deepest posteriorly, with a round snout. The eyes are large and lateral in position. The nostrils are about midway between the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally at a point below the midline at about three-fifths of the length of the body. The mouth is directed anteriorly and lacks lateral folds; one row of large labial papillae is present laterally. The beaks are moderately ovoid and finely serrate. Denticles are absent. The tail is about 70 percent of the total length. The fins are moderately deep; the ventral and dorsal fins are equal in depth, and the latter does not extend onto the body. The dorsal fin

is deepest at about three-fifths of the length of the tail. The tail terminates in a long filament. The dorsum of the body is chocolate brown, and the flanks are black. A white lateral stripe below the eye extends onto the proximal ventrolateral caudal musculature. The belly is black with cream longitudinal dashes. The tail is black with fins clear proximally and black distally.

Tadpoles were found in deep forest pools and in forest-edge pools, where they apparently swim about amidst sparse vegetation.

Mating Call.—The call consists of a harsh primary note, usually followed by 2-7 ($\bar{X}$ =3.4) shorter, secondary notes. Analysis of nine recordings made at Santa Cecilia indicates that the repetition rate of primary notes is 17.1-120.0 ($\bar{X}$ =77.9) notes per minute. The duration of primary notes is 0.11-0.35 (0.19) sec and of secondary notes, 0.03-0.06 ($\bar{X}$ =0.045) sec. The pulse rate is 100-180 ($\bar{X}$ =118.3) pulses per second. There are three harmonics, of which the fundamental at 1913-2522 ($\bar{X}$ =2304) Hz is emphasized.

Food.—Only three individuals contained identifiable food items. One frog contained a beetle (Coleoptera), another a roach (Blattidae), and another two moths (Lepidoptera).

Remarks.—Breeding congregations of *H. leucophyllata* and *H. sarayacuensis* are mutually exclusive in forest ponds, although occasionally, calling males of one species are present at ponds where the other species is calling. *Hyla leucophyllata* has not been found at ponds in primary forest, where *H. sarayacuensis* is abundant.

Hyla marmorata (Laurenti)

(PLATE 2)

Bufo marmorata Laurenti, 1768, Synop. Rept., p. 29 [Type locality.—Surinam].

Hyla marmorata—Daudin, 1802, Hist. Nat. Rain. Gren. Crap., p. 34. Bokermann, 1964, Senck. Biol., 45:250.

Material.—Lago Agrio, 26; Santa Cecilia, 54+7.

Identification.—This distinctive tree frog differs from all other frogs in the area by having a white or yellow belly with black spots or mottling and scalloped dermal fringes on the outer edges of the hands and feet.

The snout is round in dorsal view and in profile. A tympanum is present. The outer finger is webbed to the base of the disc; the other fingers are about two-thirds webbed. The toes are webbed to the bases of the discs. Breeding males lack horny nuptial excrescences. Scalloped dermal folds are present on the outer edges of the feet, forearms, and hands. The skin on the dorsum is weakly tuberculate and that on the venter is granular. The dorsum varies from grayish tan to greenish tan with black, dark brown, or reddish brown mottling that usually encloses olive-green areas dorso-laterally. In most individuals, there is a pair of large brown or reddish brown scapular marks. The axilla, groin, and posterior surfaces of the thighs are orange-yellow with black spots or mottling on the thighs. The anterior surfaces of the thighs are pale greenish yellow with black spots. The chin and belly are white or pale yellow with black spots; the ventral surfaces of the limbs are dark gray to black. The webbing is orange distally and black proximally. The iris is pale gray with fine black reticulations and a median horizontal reddish brown streak. ♂ 43 mm; ♀ 55 mm.

Occurrence.—About two-thirds of the individuals from Santa Cecilia were around temporary ponds and water-filled ditches in clearings near forest. Six were on limbs of trees in secondary forest, and two were in primary forest. At Lago Agrio, the frogs jumped out of the branches of trees felled in primary forest. Many of the frogs had been at heights of more than 20 m. *Hyla marmorata* is an arboreal forest inhabitant, but individuals migrate to breeding sites in clearings. The frogs were found in February

through July and October through December.

Life History.—*Hyla marmorata* breeds sporadically after heavy rains. After some rains, numerous adults congregate at breeding sites, but after other equally heavy rains no congregations occur. Males call from the ground, grasses, herbs, or low trees adjacent to temporary pools. Gravid females were found in February (2), April (1), May (6), July (1), October (4), and December (1). Ten females having snout-vent lengths of 46.0-53.0 ($\bar{X}$ =49.3) mm contained 630-1580 ($\bar{X}$ =1146) mature ovarian eggs. Six females having snout-vent lengths of 48.0-53.0 ($\bar{X}$ =49.8) mm deposited 740-1580 ($\bar{X}$ =1170) eggs in the laboratory. The pigmented eggs, 1.5-2.0 ($\bar{X}$ =1.7) mm in diameter, were deposited as a surface film on the water. They required 32-48 hrs to hatch; hatchlings had total lengths of 5.0-5.5 ($\bar{X}$ =5.1) mm. The smallest metamorphosed young had a snout-vent length of 14.5 mm.

Tadpoles.—The following description is based on tadpoles (KU 109423) in stage 27 having body lengths of 9.0 mm and total lengths of 25.0 mm. The body is ovoid, widest at midlength, deepest posteriorly, and with a round snout. The eyes are large and lateral; the nostrils are about one-third of the distance from the tip of the snout to the orbits. The opening of the sinistral spiracle is directed posterodorsally just below the midline at about two-thirds of the length of the body. The mouth is anterior and lacks lateral folds. The mouth, except for a bare upper lip, is bordered by one row of small labial papillae. The beaks are robust and bear fine serrations; rows of denticles are absent. The tail comprises about 64 percent of the total length and terminates in a slender point. The tail is deepest at midlength, where the dorsal and ventral fins and the caudal musculature are equal in depth. The dorsal fin does not extend onto the body. The body is olive-tan with brown transverse marks. The throat is gray with brown

flecks, and the belly is white. The caudal musculature is creamy tan with brown spots. The fins are transparent with brown spots anteriorly and black spots posteriorly. The iris is silvery white. Larger tadpoles (stages 38-40) are olive green with brown blotches dorsally. The venter is white with black flecks on the chin. There is a rectangular reddish tan blotch dorsally on the body at the base of the tail, which is heavily spotted with black.

Tadpoles were found in shallow grassy ponds and ditches.

Mating Call.—The call consists of one to three moderately long, pulsed, low notes. Analysis of ten recordings made at Santa Cecilia reveals that notes are produced at a rate of 11.5-35.3 ($\bar{X}$ =20.2) per minute. The notes have a duration of 0.11-0.27 ($\bar{X}$ =0.209) sec and 120-140 ($\bar{X}$ =130) pulses per second. The fundamental frequency is at 330-423 ($\bar{X}$ =373) Hz, and the fourth or fifth harmonic at 1320-1668 ($\bar{X}$ =1514) Hz is emphasized.

Food.—In 13 stomachs, beetles and orthopterans were the most abundant prey items (each in 38% of the stomachs). Other food items included one each — spider, mite, caterpillar, and dermapteran. The largest prey was a caterpillar 35 mm long eaten by a frog having a snout-vent length of 38 mm.

Remarks.—Recently metamorphosed young differ from adults in coloration. The dorsum is mottled dull olive-gray and black. The rump, upper arms, heels, and outer edges of the feet are creamy gray. The hands, forearms, thighs, and shanks are black with narrow grayish tan transverse bars. The posterior surfaces of the thighs are brownish black. The belly is cream; the throat, chest, and ventral surfaces of the thighs are gray, and the other ventral surfaces are black. The iris is grayish white.

Hyla minuta Peters

(PLATE 2)

Hyla minuta Peters, 1872, Monatsb. Akad.

Wiss. Berlin, 1872:680 [Type locality.—Rio de Janeiro, Brasil]. Cochran and Goin, 1970, Bull. U.S. Natl. Mus., 288:277.

Material.—Santa Cecilia, 17.

Identification.—This small brown frog characteristically has a dark brown interorbital bar and two, broad chevrons on the back. These marks and the broad transverse bars on the shanks are bordered by narrow cream lines. A transverse cream stripe is present above the anus and on each heel. These markings serve to distinguish *Hyla minuta* from other small yellowish tan or brown *Hyla* in the area, none of which has cream anal and heel stripes.

The snout is broadly rounded in dorsal view and truncate in profile. A tympanum is present; an axillary membrane is absent. The fingers are about half webbed and the toes are about three-fourths webbed. Breeding males do not have nuptial excrescences. The skin is smooth on the dorsum and granular on the belly. The dorsum is tan to pale reddish brown with dark brown to dark reddish brown markings (each narrowly bordered by cream), consisting of a broad interorbital mark, two broad chevrons on the back, and transverse bars on the forelimbs and shanks. The thighs are orange-tan. A narrow cream supra-anal stripe is confluent with transverse stripes on the heels when the frog is in a resting position. The venter is creamy white, and males have a yellow vocal sac. The iris is reddish tan. ♂ 22 mm; ♀ 24 mm.

Occurrence.—All but two individuals were found in a restricted area of disturbed forest, where they were sitting on low vegetation (<1.5 m) at night. They were found in May (3), July (8), and August (4). Two were on low vegetation at night at the edge of a pond in primary forest in June.

Life History.—Five females — May (1), July (3), August (1) — having snout-vent lengths of 23.0-24.0 ($\bar{X}$ =23.8) mm contained 160-265 (211.6) lightly pigmented eggs 1.0 mm in diameter. No

observations of breeding activity were made at Santa Cecilia, but at Belém, Brasil I have observed males of *Hyla minuta* calling from emergent vegetation in temporary ponds. Kenny (1969:47) noted in Trinidad that spawning takes place throughout the rainy season and that eggs are laid in adhesive strings or clumps on submerged leaves or debris.

Tadpoles.—The following description is based on one tadpole (KU 155522) in stage 41 having a body length of 14.2 mm and a total length of 41.7 mm. The body is ovoid, widest at midlength and deepest posteriorly. The snout is broadly rounded in dorsal view and round in profile. The eyes are large and lateral. The nostrils are about 40 percent of the distance from the tip of the snout to the orbits. The opening of the sinistral spiracle is directed posterodorsally on the midline at about two-thirds of the length of the body. The mouth is anterior and has no lateral folds. The median part of the upper lip is bare; elsewhere two rows of small labial papillae are present. The beaks are moderately robust, broad, and finely serrate. There are two lower, but no upper, rows of denticles. The tail is 68 percent of the total length and terminates in a long, slender filament. The dorsal fin extends onto the body. The tail is deepest at about midlength where the dorsal and ventral fins are equal in depth and twice as deep as the caudal musculature. The body is brown dorsally and laterally and white ventrally with brown ventrolateral flecks. The tail is cream with small brown blotches and fine brown reticulations.

The tadpoles were obtained from a forest pond in October.

Mating Call.—No calling individuals were found at Santa Cecilia, but recordings of six individuals from Belém, Brasil were analyzed. The call consists of a harsh primary note, followed by 1-3 shorter secondary notes, repeated at a rate of 8-13 ($\bar{X}$ =11.0) notes per minute and having a duration of 0.07-0.23 ($\bar{X}$ =0.164) sec and 250-375 ($\bar{X}$ =290) pulses

per second. The dominant frequency is at about 3200 Hz.

Food.—Each of three individuals having snout-vent lengths of 22 mm contained caterpillars of 17, 19, and 23 mm.

Remarks.—Elsewhere *Hyla minuta* usually is abundant; however, it is not only uncommon, but also extremely restricted in its occurrence at Santa Cecilia, the only locality in Ecuador from which it is known.

Hyla parviceps Boulenger

(FIGURE 92)

Hyla parviceps Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., London, p. 393 [Type locality.—Sarayacu, Provincia Pastaza, Ecuador]. Duellman and Crump, 1974, Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 23:19.

Material.—Dureno, 2; Lago Agrio, 1; Santa Cecilia, 220+11.

Identification.—This small frog with a short, blunt snout has a reddish brown dorsum with dark brown markings and a gray and white venter with a bright orange spot on the proximal ventral surface of the shank. The only other frogs in the area having bright orange or yellow spots on the shanks are dendrobatids, all of which have truncate, expanded digits with pairs of scutes on the dorsal surface of the distal digit; furthermore, none of the dendrobatids has large dark brown marks on the dorsum. *Hyla brevifrons* and *H. bokermanni* are like *H. parviceps* in having small cream or yellow spots on dark brown thighs, but neither of those species has a spot on the ventral surface of the thigh.

The snout is short and truncate in dorsal view and in profile. The tympanic ring is visible. The axillary membrane is abbreviated or absent. The fingers are about half webbed, and the toes are about three-fourths webbed. Breeding males lack nuptial excrescences. The skin on the dorsum is smooth with scattered small tubercles; the skin on the belly is granular. At night, the dorsum is tan with faintly darker markings. By day, the dorsum is orange-tan, reddish brown or



FIG. 92.—*Hyla parviceps*. Upper: ♂, 18 mm SVL (KU 126475). Lower: ♀, 25 mm SVL (KU 126476).

brown with dark brown markings consisting of a quadrangular or λ-shaped mark anteriorly, a transverse bar in the sacral region extending onto the flanks and broad transverse bars on the forelimbs and shanks. The flanks are paler than the dorsum. The thighs are black with one or two cream spots on the anterior surfaces. A single creamy white suborbital bar is present. Narrow creamy white canthal stripes usually are evident. The venter is gray or white with a gray or black suffusion most prominent laterally on the throat and belly. The ventral surfaces of the limbs are gray with a bright orange spot proximally on the shank. Some individuals also have an orange spot in the axilla. The iris is silvery gray with a red ring around the pupil. ♂ 18 mm; ♀ 27 mm.

Occurrence.—This small *Hyla* is ubiquitous throughout the year in primary and secondary forest, where individuals perch on leaves of herbs or leaves and branches of low (< 1.5 m) bushes at night. Males call from leaves of plants in, and peripheral to, swamps in or at the edge of forest.

Life History.—*Hyla parviceps* breeds throughout the year. Gravid females were found in every month; of 175 gravid females, 28 were found in March, 30 in October and 49 in July. Duellman and Crump (1974:23) noted that at one *Heliconia*-choked pond breeding activity reached peaks in October-November and in June-July and that males ceased calling when the water level was low in the swamp. One hundred and one gravid females had snout-vent lengths of 20.0–25.5 ($\bar{X}$ =23.3) mm and contained 120–395 ($\bar{X}$ =234.1) mature ovarian eggs. The eggs are heavily pigmented and small – 1.0–1.2 ($\bar{X}$ =1.1, N =15) mm in diameter. The eggs are deposited as clumps in the water; fifteen clutches contained 165–385 ($\bar{X}$ =302.8) eggs. Hatching occurs in 1.3–2.3 ($\bar{X}$ =1.9, N =13) days, and hatchling tadpoles are 4.0–4.5 ($\bar{X}$ =4.1, N =13) mm in total length.

Tadpoles.—The following description is based on tadpoles (KU 146790) in stage 27 having body lengths of 6.2 mm and total lengths of 18.9 mm. The body is ovoid, deepest posteriorly, with a bluntly rounded snout. The eyes are large and lateral; the nostrils are about 60 percent of the distance from the snout to the eyes. The opening of the sinistral spiracle is directed posterodorsally at a point below the midline at about three-fifths of the length of the body. The mouth is anterior and lacks lateral folds. The upper lip is bare; laterally and ventrally the mouth is bordered by one row of large labial papillae. The beaks are robust and finely serrated. Denticles are absent. The tail is about 68 percent of the total length and terminates in a long filament. At midlength of the tail, the dorsal and ventral fins are equal in depth; the dorsal fin

is about three-fourths of the depth of the caudal musculature and does not extend onto the body. The body is dark brown with a broad, transverse, cream bar dorsally on the snout and another posterior to the spiracle. The tail is pinkish orange to orange-tan with dark brown mottling.

Tadpoles were found in shallow vegetation-choked temporary and semipermanent ponds.

Mating Call.—On the basis of analysis of one recording from Santa Cecilia, the call is a series of short, high-pitched notes produced at a rate of 54.5 notes per minute and having a duration of 0.12–0.14 sec and 140 pulses per second. The dominant frequency is at about 6200 Hz. The call is soft and seldom audible in mixed choruses.

Food.—In 25 stomachs, beetles (36% of stomachs) and lepidopteran larvae (32%) were the most common items; orthopterans, homopterans, dipterans, and ants each occurred in 12 percent of the stomachs. One fly and one beetle, each 8 mm in length were contained in frogs having snout-vent lengths of 22 and 26 mm. The former also contained a caterpillar 28 mm long.

Remarks.—Despite its abundance throughout the year, no individuals were found in stomachs of the many species of snakes that feed on small frogs.

Hyla punctata (Schneider)

(FIGURE 93)

Calamita punctata Schneider, 1799, *Hist. Amph.*, 1:170 [Type locality.—Surinam].

Hyla punctata—Daudin, 1802, *Hist. Nat. Rain. Gren. Crap.*, p. 41. Duellman, 1974, *Occas. Pap. Mus. Nat. Hist. Univ. Kansas*, 27:10.

Material.—Santa Cecilia, 48+8.

Identification.—This moderate-sized, primarily green *Hyla* is most easily confused with *Hyla granosa*, a green frog lacking dorsolateral stripes. *Hyla punctata* has red flecks on the dorsum and a red dorsolateral stripe bordered above by a yellowish white stripe. Furthermore, in *H. punctata* the outer finger is only



FIG. 93.—*Hyla punctata*, ♀, 39 mm SVL (KU 111785).

basally webbed, the dorsal skin is smooth, and males lack projecting prepollical spines. In *H. granosa* the outer finger is about one-third webbed, the skin on the dorsum is finely granular, and males have projecting prepollical spines. The species of *Sphaenorhynchus* differ from *H. punctata* by having much more webbing on the feet and has a pointed snout and truncate discs, whereas *H. punctata* has a tympanum and round discs. The species of *Centrolenella* all have truncate discs and gold, yellow, or white flecks on a green dorsum, and *Phyllomedusa* lack webbing on the feet.

The snout is round in dorsal view and in profile. A tympanum is present. The fingers are webbed basally, and the toes are about half webbed. Breeding males lack horny nuptial excrescences. The skin on the dorsum is smooth, and that on the venter is granular. At night the dorsum in some individuals is pale metallic red, and the flanks and limbs are pale green; others have the coloration of individuals found by day, in which the dorsum is pale green with dark red flecks and a yellowish white dorsolateral stripe bordered below by a narrow dark red stripe. The throat is green, and the belly is white; other ventral surfaces lack pigment but have a pale greenish gray appearance. The iris is white with fine black reticulations. ♂ 40 mm; ♀ 41 mm.

Occurrence.—*Hyla punctata* was found throughout the year except in December and January. Most individuals were on low (< 1.5 m) vegetation in

secondary forest, but three were in primary forest. Breeding congregations were found in clearings, forest-edge swamps, and swamps in primary and secondary forest.

Life History.—Breeding occurs in temporary and permanent ponds sporadically after heavy rains, most frequently in April-June and October-November. Gravid females were found in April (5), May (1), June (4), July (2), October (3), and November (1). Twenty females having snout-vent lengths of 35.0-41.0 ($\bar{X}=37.2$) mm contained 230-430 ($\bar{X}=325$) mature ovarian eggs. One female 36.0 mm in snout-vent length deposited 310 pigmented eggs 1.5 mm in diameter. The eggs hatched in 86 hrs; the hatchlings had total lengths of 4.0 mm. Two recently metamorphosed young had snout-vent lengths of 11.3 and 12.2 mm.

Tadpoles.—The following description is based on tadpoles (KU 152298) in stage 36 having body lengths of 11.5 mm and total lengths of 37.5 mm. The body is shallowly ovoid, wider than deep and widest at midlength. The snout is broadly rounded in dorsal view and round in profile. The eyes are large and lateral; the nostrils are midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally on the midline at about two-thirds of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare; elsewhere the lips are bordered by a single row of small papillae. The beaks are slender and bear fine serrations. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially. The tail comprises about 70 percent of the total length and terminates in a point. The tail is deepest at three-fifths of its length, where the caudal musculature is slightly shallower than the dorsal fin, and the ventral fin is two-thirds as deep as the dorsal fin, which does not extend

onto the body. The body is dark green with black flecks, and the belly is dark gray. The tail is olive green, and the iris is pale bronze.

Tadpoles were found in open water in ponds at the forest edge and in clearings.

Mating Call.—The call consists of a series of short, low-pitched notes. Analysis of four recordings made at Santa Cecilia reveals that there are 3-17 ($\bar{X}=8.4$) notes per call group. The notes are 0.15-0.67 ($\bar{X}=0.377$) sec in duration and have 60-80 ($\bar{X}=66$) pulses per second. The fundamental frequency is at 783-1130 ($\bar{X}=964$) Hz.

Food.—The stomachs of nine individuals contained four homopterans, three orthopterans, one hymenopteran, and one dipteran.

Hyla rhodopepla Günther

Hyla rhodopepla Günther, 1859, Cat. Batr. Sal. Brit. Mus., p. 112 [Type locality.—Andes of Ecuador]. Duellman, 1972, *Herpetologica*, 28:369.

Material.—Santa Cecilia, 118+14.

Identification.—The pale, yellowish tan dorsum with red flecks, broad reddish brown lateral stripe, and white labial stripe immediately distinguish this small frog from all others in the area. *Hyla riveroi* is similar to *H. rhodopepla* but lacks the distinct lateral stripe and has brown instead of red markings. In *Hyla rhodopepla* the thighs are unpigmented; other small yellowish tan or black frogs in the area have at least the dorsal surfaces of the thighs pigmented.

The snout is round in dorsal view and in profile. An external tympanum is present; an axillary membrane is absent. The fingers are about one-third webbed, and the toes are about half webbed. Nuptial excrescences are absent in breeding males. The skin on the dorsum is smooth; that on the belly is granular. At night the dorsum is pale yellowish tan with red flecks and a broad red band from the

snout to the rump. By day the dorsum is silvery white, and the flecks and band are reddish brown. A broad, creamy white labial stripe extends posteriorly on the flanks, forming the ventral border to the brown band. Narrow, irregular, diagonal brown marks are present on the shanks. The venter is pale yellow, and calling males have bright yellow vocal sacs. The iris is pinkish gray with gray predominating peripherally. ♂ 23 mm; ♀ 29 mm.

Occurrence.—Of 105 individuals bearing ecological data, all were found at night, and two were on low vegetation at the edge of a pond in a clearing, one was in an open marsh, four were on vegetation at the edge of the forest, seven were on vegetation in secondary forest, and 91 were on vegetation in and around swamps in secondary or primary forest. Males usually call from stems of emergent plants, and most frequently, they perch transversely on the stem within 20 cm of the water. The frogs are active throughout the year.

Life History.—Although gravid females were found throughout the year, *Hyla rhodopepla* must be considered to be an opportunistic breeder. A few days with no appreciable rainfall will cause a cessation of breeding activity until the next heavy rain. Of the 115 gravid females, 102 were found in five months—March (16), June (23), July (28), October (20), and November (15). Fifty-two gravid females having snout-vent lengths of 23.0-28.0 ($\bar{X}$ =26.8) mm contained 140-422 ($\bar{X}$ =285.4) heavily pigmented eggs about 1.1 mm in diameter. Forty-three clutches contained 253-526 ($\bar{X}$ =353.4) eggs, which hatched in 2.3-3.3 ($\bar{X}$ =2.9) days. Hatchling tadpoles had total lengths of 5.0-5.5 ($\bar{X}$ =5.0) mm. One female captured on 19 May 1972 mated and deposited 390 eggs in the laboratory; she was marked and released the next day. On 19 June 1972 she was recaptured; that night she deposited 260 eggs. These are the only absolute data

available on frequency of mating and oviposition in any frogs at Santa Cecilia.

Tadpoles.—The following description is based on tadpoles (KU 125917) in stage 30 having body lengths of 4.9 mm and total lengths of 16.2 mm. The body is ovoid, wider than long, widest at anterior border of orbits, and deepest posteriorly. The snout in dorsal view is broadly rounded, in lateral view, inclined anteroventrally. The eyes are large and lateral. The nostrils are about 40 percent of the distance from the snout to the eyes. The opening of the sinistral spiracle is directed posteriorly just below the midline at about three-fifths of the length of the body. The mouth is anterior and devoid of lateral folds, labial papillae, and denticles. The beaks are robust and weakly serrated. The tail comprises about 70 percent of the total length and terminates in a long filament. The tail is deepest at about midlength, where the caudal musculature and ventral fin are equal in depth and each is equal to about 65 percent of the depth of the dorsal fin, which extends onto the body. The body and tail are pale orange with scattered brown flecks.

Tadpoles were found in a variety of temporary and ephemeral ponds, ranging from relatively open forest ponds and ponds in clearings with peripheral vegetation to weed-choked shallow ditches.

Mating Call.—The call consists of a moderately high-pitched primary note followed by 3-5 shorter secondary notes. Analysis of recordings of five individuals from Santa Cecilia reveals that primary notes are produced at a rate of 4-10 ($\bar{X}$ =7.9) notes per minute and have a duration of 0.10-0.22 ($\bar{X}$ =0.15) sec and 200-220 ($\bar{X}$ =206) pulses per second. The dominant frequency is at about 3925 Hz, and a second emphasized harmonic is at about 7850 Hz.

Food.—Ten stomachs contained a variety of small arthropods including three beetles, two flies, two orthopterans, two spiders, and one each of hemiptera, lepi-

doptera, and homoptera. The largest prey item was a roach 8 mm in length contained in a frog having a snout-vent length of 19 mm.

Remarks.—Duellman (1972c) reviewed the status of *Hyla rhodopepla* and showed that it belonged in the *Hyla microcephala* group, which is widespread and species rich in the lowlands of tropical America. *Hyla rhodopepla* is the only species in the group in the upper Amazon Basin, although *Hyla mathiassoni* occurs in the llanos of central Colombia.

Hyla riveroi Cochran and Goin

(FIGURE 94)

Hyla riveroi Cochran and Goin, 1970, Bull. U. S. Natl. Mus., 288:284 [Type locality.—Letícia, Amazonas, Colombia].

Material.—Santa Cecilia, 10.

Identification.—This small, yellowish tan frog has a brown canthal stripe and two or three cream spots on the upper lip. The canthal stripe continues as a dorsolateral stripe to the scapular or sacral regions, and tan pigment is present as a narrow stripe on the dorsal surface of the thigh. Other small hylid frogs in the area having pale markings on the upper lip include *H. bokermanni*, *brevifrons*, and *parviceps*, all of which have cream or yellow spots on dark thighs. Furthermore, the labial markings consist of one (*H. parviceps*) or two (*H. bokermanni* and *H. brevifrons*) distinct sub-orbital, vertical bars. Superficially *H. riveroi* resembles *H. rhodopepla*, in which the thighs are unpigmented, the dark stripe is lateral and extends to the groin, and the lips are white. The small yellowish tan *H. rossalleni* lacks labial markings.

The snout is round in dorsal view and in profile. The tympanic ring is evident ventrally. An axillary membrane extends about three-fourths of the length of the upper arm. The fingers are about one-fourth webbed, and the toes are about two-thirds webbed. Breeding males do



FIG. 94.—*Hyla riveroi*, ♂, 20 mm SVL (KU 126341).

not have nuptial excrescences. The skin is smooth on the dorsum and granular on the belly. At night the dorsum is pale yellow with tan markings. By day, the dorsum is tan with brown markings consisting of flecks on the back, transverse bars on the limbs, and indistinct canthal and supratympanic stripes. In most individuals some form of a brown mark is present in the occipital-scapular region. The edge of the lower lip and two or three round labial spots below the eye are pale yellow. The dorsal surfaces of the thighs are tan; other surfaces of the thighs, ventral surfaces of the limbs, and the posterior part of the belly are unpigmented. The anterior part of the belly is white. Males have yellow vocal sacs. The iris is pale red at night, changing by day to pale dull bronze with brown flecks and an orange ring around the pupil. ♂ 20 mm; ♀ 23 mm.

Occurrence.—One individual was about 3 m above the ground on a branch in secondary forest; eight were on low vegetation in swamps in secondary forest, and one was on low vegetation in a clearing. All were found at night in March through June.

Life History.—Males were calling from emergent vegetation in forest swamps in March, April, and June. The single female contained only small ovarian eggs. Presumably this species is a sporadic breeder and deposits its eggs in the water in forest swamps.

Tadpoles.—The tadpoles are unknown.

Mating Call.—Analysis of recordings of two individuals from Santa Cecilia shows the call consists of short, high-pitched, insect-like notes repeated at a rate of 37-46 ($\bar{X}=41.5$) notes per minute having a duration of 0.02-0.08 ($\bar{X}=0.053$) sec. The dominant frequency is at about 4310 Hz.

Food.—One individual contained three flies, each 5 mm in length.

Remarks.—This small frog has been found only occasionally at Santa Cecilia. Most were taken in a *Heliconia*-choked pond in the forest, where they were calling synchronously with five other small species of *Hyla*—*bokermanni*, *garbei*, *parviceps*, *rhodopepla*, and *saraya-cuensis*.

Taxonomic Comments.—The specimens were compared with a series of topotypes from Leticia, Colombia, and only slight differences in color pattern were noted. All specimens from Leticia have a dark brown dorsal blotch, whereas the blotch is replaced by brown flecks in some specimens from Santa Cecilia. All of the Ecuadorian specimens have distinct cream labial spots, whereas these are indistinct or absent in some topotypes. The species has not been reported previously from Ecuador.

Hyla rossalleni Goin

Hyla rossalleni Goin, 1959, Copeia, 1959(4): 340 [Type locality.—Leticia, Comisaria Amazonas, Colombia]. Duellman, 1974; Ocas, Pap. Mus. Nat. Hist. Univ. Kansas, 27:12.

Material.—Santa Cecilia, 8+1.

Identification.—This small, yellowish tan tree frog has a narrow brown interorbital bar and variable narrow brown markings on the body, consisting of two transverse bars or chevrons, or one bar or chevron and a longitudinal mark posteriorly. Of the frogs at Santa Cecilia it can be confused most easily with *H. riveroi*, which has cream spots on the upper lip, and *H. minuta*, which has

cream anal and heel stripes; cream spots and stripes are absent in *H. rossalleni*. The dorsal pattern of *H. rossalleni* is similar to that of *H. bokermanni*, but the latter has yellow spots on dark brown thighs and two cream labial bars; the thighs in *H. rossalleni* are unpigmented except for a narrow tan stripe dorsally.

The snout is round in dorsal view and in profile. A tympanum is present. An axillary membrane extends about two-thirds of the length of the upper arm. The fingers are about half webbed, and the toes are about three-fourths webbed. Breeding males lack nuptial excrescences. The skin is smooth on the dorsum and granular on the venter. The dorsum is yellowish tan with a narrow dark brown interorbital mark and two narrow transverse dark brown bars on the back. The dorsal surfaces of the limbs are yellowish tan with faint brown transverse bars on the limbs. The anterior and posterior surfaces of the thighs and the flanks are pale dull yellow. The upper lip is tan with yellow mottling. The venter is white, and the iris is pale metallic red. ♂ 20 mm.

Occurrence.—A single male was on low vegetation in a swamp in secondary forest on the night of 7 June 1968, and seven were on low vegetation in a clearing on the night of 2 June 1975.

Life History.—Nothing is known. Presumably eggs are deposited in the water or on vegetation over the water in forest ponds.

Tadpoles.—The following description is based on tadpoles (KU 155521) in stage 36 having body lengths of 7.0 mm and total lengths of 19.2 mm. The body is ovoid, wider than deep, widest at mid-length, and deepest posteriorly. The snout in dorsal view is broadly rounded, and in profile it is round. The eyes are large and lateral; the nostrils are midway between the snout and the orbits. The opening of the sinistral spiracle is directed posteriorly below the midline at about two-thirds of the length of the body. The mouth is anteroventral with

lateral folds and one row of labial papillae, except on the median part of the upper lip, which is bare. The beaks are moderately robust and bear long, fine, serrations. There are two upper and three lower rows of denticles; the second upper row is narrowly interrupted medially. The tail comprises about 65 percent of the total length and terminates in a filament. The tail is deepest at mid-length where the ventral fin is slightly shallower than the dorsal fin and the caudal musculature equals about 65 percent of the dorsal fin, which extends onto the body. The body is tan with a dark brown lateral stripe from the snout, through the eye and extending the entire length of the tail. The caudal musculature is tan and the fins translucent, both with small brown flecks.

Tadpoles were found amidst vegetation in a shallow pond in secondary forest.

Mating Call.—The call is unknown.

Remarks.—This species has not been reported previously from Ecuador. The tadpoles described herein are assigned to *Hyla rossalleni* on the advice of Ronald Altig, who collected them in October 1973.

Taxonomic Comments.—I have examined specimens referred to this species from numerous localities in Colombia, Ecuador, Perú, Bolivia, and western Brasil. The variation in dorsal coloration is great but always consists of irregular dark brown dashes, interconnected or not, so as to form an H- or X-shaped mark in the scapular region. Other specimens, such as the one from Santa Cecilia, have only longitudinal or diagonal dashes on the back.

Hyla rubra Laurenti

(FIGURE 95)

Hyla rubra Laurenti, 1768. Synop. Rept., p. 35 [Type locality.—"America"]. Cochran and Goin, 1970, Bull. U. S. Natl. Mus., 288:239.

Material.—Puerto Libre, 14; Santa Cecilia, 151+17.



FIG. 95.—*Hyla rubra*, ♀, 43 mm SVL; Mera, Provincia Pastaza, Ecuador (KU 120922).

Identification.—*Hyla rubra* differs from all other frogs in the area by having bold black or dark brown mottling enclosing numerous yellow spots in the groin and on the anterior and posterior surfaces of the thighs. In other members of the *Hyla rubra* group, these surfaces are uniform pale green (*H. cruentomma*) or yellow or pale green with brown spots or streaks (*H. funerea*).

The snout is acutely rounded in dorsal view and in profile and protrudes beyond the margin of the lip. A tympanum is visible. Webbing is absent between the fingers, and the toes are about three-fourths webbed, except that the webbing is vestigial between the first and second toes. Nuptial excrescences are absent in breeding males. The skin on the dorsum is smooth; that on the belly is granular. At night the dorsum is pale dull yellow with or without faint tan markings. By day the dorsum is tan, brown, or grayish green, usually with distinct creamy tan or pale yellow dorsolateral stripes extending from the eyelids to the sacral region. A narrow, irregular, tan, middorsal stripe is present in some individuals. Faint darker brown transverse bars usually are evident on the dorsal surfaces of the shanks and feet. The anterior and posterior surfaces of the thighs are dark brown or black with yellow spots. In most individuals the black and yellow marking also is present in the groin, and in a few individuals black mottling enclosing yellow spots is present on the flanks. In most individuals the flanks are

yellow, and in some the groin is yellow. The venter is creamy white except for a yellow vocal sac in males. The iris is bronze with black reticulations. ♂ 36 mm; ♀ 44 mm.

Occurrence.—This species is extremely abundant at Santa Cecilia, where it is active throughout the year. No individuals were found in primary forest; only 42 percent of 146 frogs were found in disturbed, cut-over forest, whereas the others were in clearings. Although most of the frogs in cut-over forest were on low (< 1.5 m) vegetation at night; eight were on branches higher than 1.5 m. Seventeen individuals were found beneath stones or logs in clearings by day; all others were found at night. Although most individuals in clearings at night were perched on low bushes or grasses in, or adjacent to, temporary ponds, some were sitting on bare ground next to water. The frogs are extremely wary, leaping into dense vegetation or running across the ground or up tree trunks in order to avoid capture.

Life History.—Except for dry moonlit nights, males call throughout the year. Large numbers of gravid females were found throughout the year, except the driest months, August and December, when no females were found. Apparently, with the exception of dry periods of a few days at a time and during full moon, *Hyla rubra* breeds after heavy rains throughout the year. Sixty-six females having snout-vent lengths of 35.0–43.5 ($\bar{X}=39.5$) mm contained 68–960 ($\bar{X}=521$) mature ovarian eggs about 1.5 mm in diameter. In the laboratory three individuals, 40.0–42.0 ($\bar{X}=40.8$) mm in snout-vent length deposited clutches of 745–807 ($\bar{X}=777$) pigmented eggs 1.5 mm in diameter as surface films on the water. The eggs required 48–55 hrs to hatch; the hatchlings had total lengths of 4.5–5.0 ($\bar{X}=4.7$) mm.

Tadpoles.—Tadpoles (KU 109492) in stage 36 have body lengths of 8.4 mm and total lengths of 24.3 mm. The body is ovoid, slightly wider than deep, widest

medially, and deepest posteriorly. The snout is bluntly rounded in dorsal view and round in profile. The eyes are large and lateral; the nostrils are midway between the tip of the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally just below the midline about two-thirds of the length of the body. The mouth is anteroventral and has lateral folds. The median part of the upper lip is bare; elsewhere there is a single row of blunt labial papillae bordering the mouth, except that supernumerary papillae are present in the lateral folds. The beaks are robust and finely serrate. There are two upper and three lower rows of denticles; the second upper and usually the first lower rows are narrowly interrupted medially. The tail comprises about 68 percent of the total length and terminates in a fine point. The tail is deepest at midlength, where the ventral fin is slightly shallower than, and the caudal musculature is about 70 percent of, the depth of the dorsal fin, which extends onto the body. The body is iridescent silvery-gold laterally and ventrally. The dorsum and tail are yellowish tan with darker brown flecks. A brown stripe extends from the snout to the eye.

Tadpoles were found in nearly every aquatic site in clearings, including shallow grassy depressions, ditches, and temporary ponds. Also tadpoles were found in a water can and a dugout canoe. In natural situations the tadpoles swim close to the surface by day; when disturbed they seek refuge amidst aquatic vegetation.

Mating Call.—The call consists of a series (up to 10) of short notes “aah-aah-aah.” Analysis of recordings of five individuals from Santa Cecilia reveals that the notes have a duration of 0.12–0.15 ($\bar{X}=0.13$) sec and 61–65 ($\bar{X}=63$) pulses per second. The dominant frequency is between 1545 and 1640 Hz.

Food.—Examination of 25 stomachs revealed the presence of a diversity of arthropods, of which orthopterans (40%

of stomachs) were the most common prey; these are followed by caterpillars (24%), moths (20%), beetles (20%), dipterans (18%), and homopterans. There was also one hemipteran and one ant. The largest prey was a caterpillar 27 mm long eaten by a frog 34 mm in snout-vent length.

Remarks.—Although the species was not uncommon in 1966 and 1967, it was restricted to the clearings of Muñozlandia and the airstrip. Increased clearing and partial cutting of primary forest has resulted in a considerable expansion of its local range and seemingly of its abundance.

Taxonomic Comments.—The taxonomic status of many populations currently assigned to *Hyla rubra* is uncertain. Among populations studied to date, those in Surinam, northeastern Brasil, and Amazonian Ecuador exhibit differences in size, proportions, coloration, and some parameters of the mating calls. The type locality of *Hyla rubra* is being restricted to Paramaribo, Surinam, by M. J. Fouquette, Jr. *Hyla rubra huebneri* Melin, named from Taracú São Gabriel, and Manáus, Território do Amazonas, Brasil, may be the name applicable to the frogs at Santa Cecilia. However, at this time it is not certain that the Ecuadorian frogs should be recognized as the same, subspecifically distinct, or specifically distinct from those in Surinam. Until the status of the Amazonian populations is determined, it is least confusing to refer them to *Hyla rubra*.

Hyla sarayacuensis Shreve

(PLATE 2)

Hyla leucophyllata sarayacuensis Shreve, 1935, Occas. Pap. Boston. Soc. Nat. Hist., 8:215 [Type locality.—Sarayacu, Provincia Pastaza, Ecuador].

Hyla sarayacuensis—Goin, 1957.—J. Washington Acad. Sci., 47:60.

Material.—Santa Cecilia, 65+19.

Identification.—This distinctive member of the *Hyla leucophyllata* group has

orange webbing and hidden surfaces of the thighs. The dorsum is mottled dark and light brown with creamy white to golden yellow markings consisting of a broad mark on the top of the head anterior to the eyes, a diagonal mark extending from the eyelid to the midflank, and diagonal marks on the shanks. All of the light markings have irregular edges. A pair of small cream spots in the sacral region and a larger cream spot on the rump usually are present. *Hyla leucophyllata*, which also has orange flash colors, has broad dorsolateral light areas and light spots on the snout and rump delineating a dark brown hour-glass-shaped middorsal mark. The edges of the pale markings are regular, and the dorsal surfaces of the shanks are uniformly pale, or marked by one or two narrow, dark crossbars. *Hyla bifurca* differs from *H. sarayacuensis* by having narrow parallel dorsolateral stripes, a pale spot on the rump and each heel, and no pale transverse marks on the shank. Of the other members of the *Hyla leucophyllata* group, *H. favosa* has orange flash colors and a network of creamy white lines on the dorsum, and *H. triangulum* has pink or red flash colors and a pale dorsum with or without one or more brown spots. Females of species belonging to the *Hyla parviceps* group (*H. bokermanni*, *brevifrons*, and *parviceps*) have broad diagonal dorsolateral stripes, but these small frogs have dark thighs with pale spots on the anterior or dorsal surfaces, whereas the thighs are pale orange in *H. sarayacuensis*.

The snout is broadly rounded in dorsal view and truncate in profile. An axillary membrane extends to about the midlength of the upper arm. The fingers are about half webbed and the toes about two-thirds webbed. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsum is brown, with or without paler brown marbling; pale golden markings consist of a triangular mark on the top of the head anterior to the eyes, broad diagonal bar

from the eye to midflank, a pair of small spots in the sacral region, a large spot on the rump, and a diagonal bar on each flank. The markings have irregular edges. Also, each elbow, knee, and heel usually has a large golden yellow spot, and there may be a golden transverse bar on the forearm and numerous golden flecks on the dorsum. The sides of the head and the flanks are brown, and the belly is cream. By day, the dorsum is dark brown with creamy to silvery white markings. The hands, feet, anterior and posterior surfaces of the thighs, lower flanks, and ventral surfaces of the limbs are pale orange at night and deep orange by day. The vocal sac is yellow; males lack nuptial excrescences. The iris is coppery bronze. ♂ 27 mm; ♀ 37 mm.

Occurrence.—All individuals were found at night, and most were in forest. Adults were found on low vegetation (< 1.5 m) in primary and secondary forest. Most adults were on bushes around or emergent vegetation in forest swamps, but some were found at ponds in clearings or at the edge of the forest.

Life History.—This species is an opportunistic breeder. Males call from low vegetation (< 1.5 m) above the water in forest and forest-edge swamps after rains throughout the year. Gravid females were found in all months, except January, June, August, September, and December. Fourteen females having snout-vent lengths of 31.0-37.0 ($\bar{X}=33.6$) mm contained 68-176 ($\bar{X}=113.4$) eggs. Seven clutches contained 92-138 ($\bar{X}=113.1$) eggs, 2.0 mm in diameter. The lightly pigmented eggs are deposited on the upper surfaces of leaves over water. Females usually deposit their ovarian complement in several clutches on the same or adjacent leaves or blades of grass. Usually the eggs are about 1 m above the water. Four metamorphosing young have snout-vent lengths of 11.8-12.5 ($\bar{X}=12.2$) mm.

Tadpoles.—The following description is based on tadpoles (KU 146809) in

stage 37 having body lengths of 8.9 mm and total lengths of 22.5 mm. In dorsal view the body is violin-shaped with a bluntly rounded snout. In lateral view the body is shallowly ovoid, deepest posteriorly, with a bluntly rounded snout. The eyes are large and lateral in position. The nostrils are about 40 percent of the distance from the snout to the orbits. The opening of the sinistral spiracle is below the midline at about three-fifths of the length of the body. The mouth is anterior and lacks lateral folds. The upper lip is bare; a single row of labial papillae borders the mouth laterally and ventrally. The beaks are robust and finely serrate. Denticles are absent. The tail is about 70 percent of the total length. The fins are moderately deep, the ventral fin being slightly deeper than the dorsal fin, which does not extend onto the body. The fins are deepest at midlength of the tail, where the caudal musculature is about 85 percent of the depth of the dorsal fin. The tail terminates in a long filament. The dorsal and lateral surfaces of the body are gray to reddish brown; the belly is metallic gold. The tail is black or gray with black reticulations. The iris is reddish gold.

Tadpoles have been found in shaded forest ponds where they are pelagic in water about 1 m in depth.

Mating Call.—The call consists of a harsh primary note usually followed by one or two shorter secondary notes. In eight recordings from Santa Cecilia, the repetition rate of primary notes is 22.2-33.3 ($\bar{X}=27.0$) notes per minute. The duration of primary notes is 0.05-0.14 ($\bar{X}=0.078$) sec, and of secondary notes, 0.04-0.09 ($\bar{X}=0.06$) sec. The pulse rate is 60-80 ($\bar{X}=74.5$) pulses per second. There are three harmonics, of which the fundamental at 2826-3391 ($\bar{X}=2982$) Hz is emphasized.

Food.—Only five individuals contained identifiable food items. One frog contained a roach, and four contained moths.

Remarks.—Although occasional individuals are found amidst breeding congregations of other members of the *Hyla leucophyllata* group (*H. bifurca*, *leucophyllata*, *triangulum*) *H. sarayacuensis* breeds primarily in forest ponds, not frequented by other members of the group.

Hyla triangulum Günther

(PLATE 2)

Hyla triangulum Günther, 1868, Proc. Zool. Soc. London, 1868:489 [Type locality.—? Brasil]. Duellman, 1974, Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 27:19.

Material.—Puerto Ore, 29; Santa Cecilia, 135+11.

Identification.—This species is unique among members of the *Hyla leucophyllata* group in having pink (night) or red (day) webbing and hidden surfaces of the limbs; these flash colors are orange in the other species, all of which, except *H. favosa*, have some form of dorsolateral light stripes. The dorsum in *H. triangulum* is creamy tan with or without one or more round brown spots. The pattern in those individuals having many spots and narrow interspaces resembles that of *H. favosa*, which has a dark brown dorsum with a network of narrow creamy white lines. The only other frog in the area having red webbing is the much larger *Phrynolhyas coriacea*, which has brown thighs, a bluish black postorbital mark, a large middorsal dark brown quadrangular mark, and thick pustular skin on the dorsum.

The snout is broadly rounded in dorsal view and truncate in profile. An axillary membrane extends about two-thirds of the length of the upper arm. The fingers are about one-half and the toes about three-fourths webbed. The skin on the dorsum is smooth, and that on the belly is granular. At night the dorsum is pale yellowish tan, with or without brown markings, and the flanks are gray; the hands, feet, and hidden surfaces of the limbs are pink. By day the dorsal

surfaces of the head, body, and shanks are pale brown, pale gray, yellowish tan, or white, with or without dark brown markings. The sides of the head, flanks, and dorsal surfaces of the arms, thighs, and feet are dark brown. In males the venter is white, and the vocal sac is yellow; in females the throat and belly are pale orange-red. The fingers, toes, webbing, axillary membrane, groin, anterior and posterior surfaces of the thighs, and ventral surfaces of the limbs are red. Males lack nuptial excrescences. The iris is coppery bronze. ♂ 28 mm; ♀ 42 mm.

The variation in color pattern morphs was analyzed for 1595 adults from Limoncocha, Ecuador, by Duellman (1974a), who showed that 55.3 percent of the specimens had no dorsal markings, 14.1 percent had one dark spot in the occipital region, and 14.6 percent had middorsal spots from the occiput to the rump. Only 1.9 percent of the specimens had spots scattered over the entire dorsum. In the last two morphs the dark brown on the sides of the head, flanks, and dorsal surfaces of the shanks is fragmented into spots. Approximately the same percentages of color morphs occur at Santa Cecilia, but the heavily spotted morph is slightly more abundant (6.6%, 8 of 120 adults).

Occurrence.—This species inhabits a variety of non-forest situations; only 19 percent of 158 individuals was found in secondary forest, and none was in primary forest. Breeding congregations were found in temporary ponds and ditches in clearings and partially cleared areas and along the cleared shore of a lake.

Life History.—Males call throughout the year from low vegetation in and around temporary or permanent bodies of water in clearings. Gravid females were found in every month of the year except September. Twenty-three gravid females having snout-vent lengths of 36.0-41.5 ($\bar{X}$ =39.5) mm contained 320-650 ($\bar{X}$ =501.7) eggs. Nine clutches con-

sisted of 465-690 ($\bar{X}$ =550.9) eggs. The heavily pigmented eggs are deposited on the upper surfaces of leaves of emergent vegetation, usually less than 30 cm above the water. Four metamorphosing young have snout-vent lengths of 11.6-11.9 ($\bar{X}$ =11.8) mm.

Tadpoles.—Tadpoles (KU 146810) in stage 35 have body lengths of 7.5 mm and total lengths of 15.2. In dorsal view the body is robustly violin-shaped with a broadly rounded snout; in lateral view, shallowly ovoid, deepest posteriorly, with a round snout. The eyes are large and lateral. The nostrils are about midway between the snout and the orbits. The opening of the sinistral spiracle is directed posterodorsally on the midline about two-thirds of the length of the body. The mouth is anterior and lacks lateral indentations. The upper lip is bare, and the mouth is bordered laterally and ventrally by a fleshy fold. The beaks are moderately robust and finely serrate. Denticles are absent. The tail is about 67 percent of the total length. The fins are moderately deep, the dorsal fin being three-fourths of the depth of the ventral fin and not extending onto the body. The fins are deepest at about two-thirds of the length of the tail, at which point the caudal musculature is about as deep as the dorsal fin. The tail terminates in a long filament. The body is dark brown with a broad pale tan dorsolateral stripe, white ventrolateral stripe, and two short silvery stripes on the anterior part of the belly. The tail is boldly marked by two broad vertical black bars, the proximal one only on the caudal musculature, and the distal one extending to the periphery of the fins. Otherwise the tail is unpigmented. The iris is reddish bronze.

Tadpoles have been found amidst vegetation in shallow areas of ponds in clearings.

Mating Call.—The call consists of a harsh primary note usually followed by 2-6 ($\bar{X}$ =3.7) shorter secondary notes. Analysis of four records from Santa Cecilia revealed that the repetition rate of

primary notes is 12.0-31.6 ($\bar{X}$ =21.8) notes per minute. The duration of primary notes is 0.08-0.34 ($\bar{X}$ =0.17) sec, and of secondary notes is 0.02-0.06 ($\bar{X}$ =0.036 sec. The pulse rate is 160-180 ($\bar{X}$ =176) pulses per second. There are 7 or 8 harmonics, the fundamental being at 411-625 ($\bar{X}$ =512) Hz; the third to fifth harmonic at 1875-2680 ($\bar{X}$ =2299) Hz is emphasized.

Food.—Stomachs of 24 specimens contained food. Orthopterans (25% of stomachs) and lepidopterans (21%) were the most abundant items, followed by dipterans (17%), beetles (12%), and spiders (8%). The largest prey items, a fly 16 mm long and a beetle 15 mm long, had been eaten by frogs having snout-vent lengths of 36 and 39 mm, respectively.

Taxonomic Comments.—The different color morphs of this species have received six specific names. The taxonomy of the species was studied by Duellman (1974a).

Remarks.—*Hyla triangulum* and *H. bifurca* frequently call from the same sites at the same time. Although males of the two species are about the same size, females of *H. triangulum* attain lengths of 42 mm, whereas those of *H. bifurca* do not exceed 35 mm. Noticeable differences exist in three parameters of the mating calls; the call of *H. triangulum* has a faster pulse rate, slower note repetition rate, and lower dominant frequency. These differences in calls and the difference in size of the females probably are effective premating isolating mechanisms in these two related species.

Nyctimantis rugiceps Boulenger

(FIGURE 96)

Nyctimantis rugiceps Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., London, p. 421 [Type locality.—Canelos, Provincia, Pastaza, Ecuador].

Material.—Lago Agrio, 1; Santa Cecilia, 9.

Identification.—This large tree frog



FIG. 96.—*Nyctimantis rugiceps*, ♂, 63 mm SVL (KU 125960).

is distinctive in having a pale grayish tan dorsum and dark brown flanks, venter, and hidden surfaces of the limbs with large yellow spots on the flanks and thighs. Other large frogs in the area with dark brown ventral surfaces have a green dorsum (*Phyllomedusa*) or a triangular head with a fleshy proboscis (*Hemiphractus*); no other species has large yellow spots on dark brown flanks.

The head is nearly as broad as long; the skin is co-ossified with the underlying cranial elements. Webbing is absent on the hand, and the toes are about half webbed. The skin on the dorsum is smooth, except for rugosities on the head; that on the belly is granular. A large external tympanum is present. The dorsum varies from gray to tan, although one individual was dark brown above at night; in some individuals the periphery of the dorsum has a bronze tinge. The flanks, hidden surfaces of the limbs, and all ventral surfaces are dark chocolate brown. One to three large, ovoid spots are present on the flanks and one large spot is present on the posterodorsal surface of each thigh. These spots are bright yellow to lemon yellow. The iris is dark brown. Breeding males have dark brown nuptial excrescences on the thumbs. ♂ 65 mm; ♀ 61 mm.

Occurrence.—Most individuals were associated with clumps of bamboo, which is more abundant in secondary forest than in primary forest. Except for one

female obtained from a felled tree at Lago Agrio by day, all were found at night. Two subadults were on bushes (< 1.5 m); all others were males calling from water-filled cavities in trees or more commonly in bamboo. Males were heard calling from heights of more than 10 m.

Life History.—The major clue to the life history of *Nyctimantis* is the calling behavior of the males. The distinctive call was heard sporadically throughout the year. The males seem to be widely scattered throughout the forest and remain in one place for lengthy periods of time. Apparently the same individual was heard nightly from the same clump of bamboo for two or three weeks. Calling males were found in bamboo stumps (3), in bamboo sections (2), and in a cavity in a tree (1). The bamboo stumps were about 10 cm in diameter, and each contained 10-20 cm of water. The frogs called from the inner walls or edge of the bamboo; upon being disturbed they submerged. Some large bamboos at angles of about 45° have cracks in the walls, and males are able to enter the hollow stalks containing some water. In September 1973 Ronn Altig found 773 eggs in a bamboo stump inhabited by a calling male; he found eggs in another stump in June 1975. Attempts to maintain the eggs was unsuccessful.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call consists of two or three loud notes "knock-knock." Analysis of four recordings made at Santa Cecilia revealed that the call rate is 2.3-2.4 calls per minute with 4.7-9.1 ($\bar{X}=5.8$) notes per minute. Three individuals produced only two notes per call group, whereas the fourth frog gave two or three notes. Usually the second note is much longer than the first, which has a duration of 0.04-0.15 ($\bar{X}=0.105$) sec; the duration of the second notes is 0.05-0.76 ($\bar{X}=0.256$) sec. There are approximately 100 pulses per second. The fundamental frequency at 478-1130 ($\bar{X}=847$) Hz is dominant.

Food.—Two individuals contained food; one had eaten a large roach and the other a grasshopper.

Remarks.—The accumulated knowledge about this monotypic genus, which is endemic to Amazonian Ecuador, was summarized by Duellman and Trueb (1976).

***Osteocephalus buckleyi* (Boulenger)**

(FIGURE 97)

Hyla buckleyi Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.:362 [Type locality.—Canelos, Provincia Pastaza, Ecuador].

Osteocephalus buckleyi—Goin, 1961, Ann. Carnegie Mus., 36:13. Trueb and Duellman, 1971, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 1:19.

Material.—Lago Agrio, 1; Puerto Libre, 1; Santa Cecilia, 7.

Identification.—This moderate-sized tree frog is unique in the area by having areolate skin on the anterior part of the flanks. There the skin is elevated amidst an irregular network of depressions. Other species of *Osteocephalus* are larger and are predominantly brown dorsally, whereas *O. buckleyi* is green with brown or black markings. *Osteocephalus buckleyi* differs from other green sympatric species by having tubercular skin dorsally.

The snout is truncate, and the head is nearly as long as wide. The fingers are about one-third webbed, and the feet are about two-thirds webbed. The skin on the dorsum in males bears a mixture of large and small, non-spinous tubercles, whereas in adult females tubercles are present on the eyelids and supratympanic fold and scattered on the back. The skin on the belly is granular and that on the anterior flanks is areolate. The tympanum is at least two-thirds the size of the eye. The dorsum is pale green with dark irregular blotches; a narrow yellow or tan middorsal stripe is present or not. The flanks are cream to tan with tan to black blotches. The anterior surfaces of the thighs are dark brown, and the dorsal and posterior surfaces of the



FIG. 97.—*Osteocephalus buckleyi*, ♂, 45 mm SVL (KU 123171).

thighs and shanks are dull green, or tan with darker green or brown blotches. In some individuals a dull blue tint is present on the anterior and posterior surfaces of the thighs. The webbing is brown. A broad, black postorbital bar encompasses the tympanum, and a broad pale green suborbital bar extends to the lip. The venter is grayish brown in appearance; the tips of the granules are white, and the intergranular spaces are brown. The iris is golden or greenish bronze with black flecks or bars ventrally and a median horizontal brown streak. Breeding males have dull brown nuptial excrescences. ♀ 45 mm; ♂ 49 mm.

Occurrence.—Ecological data accompany only seven of the nine specimens, which were obtained in March (1), May (2), June (1), and July (5). All were on low vegetation in primary forest (5) or at the edge of forest (2) at night.

Life History.—A female containing 580 mature ovarian eggs was found on 12 May. No breeding activity was observed.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The mating call is unknown.

Food.—One individual contained a roach, and another had eaten a dipteran.

Remarks.—Trueb and Duellman (1971) presented a detailed discussion of the species.



FIG. 98.—*Osteocephalus leprourii*, ♀, 62 mm SVL (KU 125962).

Osteocephalus leprourii
(Duméril and Bibron)

(FIGURE 98)

Hyla leprourii Duméril and Bibron, 1841, Erpetol. Gen., 8:553 [Type locality.—“Cayenne”].

Osteocephalus leprourii—Goin, 1961, Ann. Carnegie Mus., 36:13. Trueb and Duellman, 1971, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 1:25.

Material.—Lago Agrio, 36; Puerto Libre, 2; Santa Cecilia, 58.

Identification.—Adults of this species are readily distinguished from other hylid frogs in the upper Amazon Basin by the combination of a pale brown dorsum with narrow dark brown transverse bars, a pale cream labial stripe expanded into a suborbital blotch, and finely tuberculate dorsal skin in males. Only *Hyla lanciformis* has similar dorsal coloration, but that much larger frog has a pointed snout, smooth dorsal skin, and a brown throat and chest, whereas *O. leprourii* has a bluntly rounded snout and a creamy white venter. Due to vagaries of coloration, some individuals of *O. leprourii* and *O. taurinus* can be confused. The larger *O. taurinus* has more webbing on the hand, larger dorsal tubercles in the males, no expanded suborbital cream spot, and usually small round dark spots on the flanks. Juveniles are tan with cream dorsolateral stripes, thereby resembling juveniles of *Hyla alboguttata*, which differ most noticeably

by lacking dark transverse bars on the limbs.

The snout is bluntly rounded. The head is flat and nearly as wide as long. The tympanum is about three-fourths of the diameter of the eye. The dorsal skin is smooth in females but in males bears numerous, minute, spinous tubercles. The fingers are about one-fourth webbed and the toes three-fourths webbed. In males the dorsal ground color varies from dark brown to ochre-tan; the transverse dark brown bars on the dorsum vary from six to 12, with the one across the eyelids being broader than the others. In some individuals, narrow bars alternate with wider ones, and in some of these, the narrow bars do not extend so far laterally as the wider ones. Alternating wide and narrow transverse bars are present on the forearms and shanks. The flanks are uniform tan to creamy white. The labial area is creamy white and expanded posteriorly into a suborbital spot. Most individuals have dark brown anal stripes bordered above by a cream line. The venter is unmarked salmon, tan, or white. The iris is bronze with a greenish cast and black reticulations. Breeding males have dark brown nuptial excrescences. In females the dorsal color is the same as that in males, except that the dark marks tend to be outlined with cream; the venter is salmon-tan. ♂ 49 mm; ♀ 64 mm.

Occurrence.—Most of the adults (34) were obtained in May from tops of trees as they were felled in primary forest at Lago Agrio. Two were obtained in secondary forest at Puerto Libre in July. At Santa Cecilia one each was obtained in May, June, July, and September; two were in primary forest and two in secondary forest. At Puerto Libre and Santa Cecilia the frogs were on bushes and trees at night. Juveniles were found from March through November in primary forest (14), secondary forest (24), and at the forest edge (5).

Life History.—Fifteen gravid females from May contained 480-1150 ($\bar{X}$ =839)

mature ovarian eggs. No other gravid females were found. On 12 May at Lago Agrio, males were calling from branches of fallen trees over a temporary pool, and a male called nightly from 4 to 17 July from a large tree at Puerto Libre. Juveniles were found in March (3), April (1), May (2), June (9), July (31), August (4), September (2), October (1), and November (1). The largest juvenile (37 mm) was found in May, and a metamorphosing young was found in June. The wide range of dates for the collection of juveniles suggests a more lengthy breeding season than do the limited observations on dates of calling. On the basis of the one chorus observed, it is assumed that the eggs and larvae develop in ponds in the forest.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call is a soft rattling chuckle.

Food.—In 25 stomachs, orthopterans were the most abundant food item (36% of the stomachs), followed by Coleoptera (20%), roaches (16%), Lepidoptera (8%), coleopteran larvae (8%), spiders (8%), Dermaptera (8%), Diptera (4%), and ants (4%).

Remarks.—The striking ontogenetic change in coloration was illustrated by Trueb and Duellman (1971: 29). Juveniles having snout-vent lengths of less than 28 mm have an olive-brown dorsum with a pale cream stripe across the head and broad cream dorsolateral stripes; transverse dark bars are absent. Individuals 30–35 mm in length have dark brown transverse bars on the limbs and still retain the pale dorsolateral stripes; the stripes are absent in larger individuals.

Osteocephalus taurinus Steindachner

(FIGURE 99)

Osteocephalus taurinus Steindachner, 1862, Arch. Zool. Anat. Fisio., 2:77 [Type locality.—Barra do Rio Negro, Manaus. Território do Amazonas, Brasil]. Trueb and Duellman, 1971, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 1:31.



FIG. 99.—*Osteocephalus taurinus*, ♂, 81 mm SVL (KU 126652).

Material.—Lago Agrio, 9; Santa Cecilia, 13.

Identification.—This large tree-frog with paired lateral vocal sacs and tubercular dorsal skin in males can be confused only with the smaller *O. leprourii*, males of which have more numerous and smaller tubercles on the dorsum. *Osteocephalus taurinus* has irregular dark dorsal blotches and usually round brown or black spots on the flanks, whereas *O. leprourii* has transverse dark bars dorsally and unmarked flanks. Other large brown tree frogs in the area (*Hyla boans*, *geographica*, and *lanciformis*) have single, median, subgular vocal sacs, prepollical spines, and smooth skin on the dorsum.

The snout is bluntly rounded, and the head is nearly as wide as long. In large individuals, the skin on the top of the head is co-ossified with the underlying cranial elements; a pair of frontoparietal ridges is evident. The tympanum is about three-quarters of the diameter of the eye. The fingers are about half webbed, and the toes are four-fifths webbed. The dorsal skin is smooth in females, and in males bears many moderately large spinous tubercles. The dorsum is tan to dark brown (rarely olive green) with irregular dark brown blotches. A few individuals have either a narrow yellow middorsal stripe or small white spots scattered on the dorsum. Broad dark brown bars are present

on the forearms, shanks, and feet. The flanks are tan to yellow with dark brown or black spots or mottling. The venter is creamy white to pale tan with or without brown flecks or spots on the throat and chest. The margin of the upper lip is pale green to creamy yellow. The iris is greenish bronze with bold, radiating black reticulations. Breeding males have dull nuptial excrescences. ♂ 81 mm; ♀ 90 mm.

Occurrence.—Three of 22 specimens were in secondary forest; the others were in primary forest. At Lago Agrio five frogs were taken from tops of trees as they were felled. All others were found on bushes and trees at night. Except for one individual collected in November, all were found in April through August.

Life History.—The only chorus of this species was encountered at Lago Agrio on 12 May. Males were calling from the ground adjacent to a small pool. Upon being disturbed, the frogs jumped onto limbs and scampered up trees, quickly ascending to heights of 3-4 m. Only one female (from July) was gravid; she contained 550 ovarian eggs. According to Bokermann (1964) eggs are deposited in a film on the surface of flooded depressions in the forest. Duellman and Lescure (1973) noted the presence of tadpoles in Pastaza Province, Ecuador, in July; in Amazonas, Brasil, in June; and in French Guiana in February and June.

Tadpoles.—Tadpoles are not available from Santa Cecilia; the following description is based on a specimen (KU 148706) in stage 37 and having a body length of 18.3 mm and a total length of 48.5 mm from Kérenroch, French Guiana. The body is elongately elliptical with a round snout, two-thirds as wide as deep, and deepest posteriorly. In profile the snout is narrow and round. The eyes are small, widely separated, and directed laterally. The nostrils are directed anterolaterally about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is

directed posterodorsally just below the midline at about midlength of the body. The cloacal tube is short and dextral. The caudal musculature is moderately slender. The caudal fins are about equal in depth, deepest at about two-fifths of the length of the tail; the dorsal fin does not extend onto the body. The moderately small mouth is directed ventrally. The median third of the upper lip is bare; the rest of the mouth is bordered by two rows of small labial papillae. The beaks are slender, bearing small, blunt serrations; the upper beak forms a broad arch with long, slender lateral processes, whereas the lower beak is broadly V-shaped. There are three upper and five lower rows of denticles. The tail is about 63 percent of the total length and is acutely rounded terminally. The tadpoles are entirely black.

Mating Call.—The call is a loud "boop-boop-boop," followed or not by "worr." Both kinds of notes were analyzed by Duellman and Lescure (1973) from a recording made at Limoncocha, Ecuador.

Food.—Examination of ten stomachs revealed that orthopterans were present in eight and roaches in two. One example of each of three other anthropods was found: ant, pedipalpid, and spider.

Phrynohyas coriacea (Peters)

(FIGURE 100)

Hyla coriacea Peters, 1867, Monatsb. Akad. Wiss. Berlin, 1867:711 [Type locality.—"Surinam"].

Phrynohyas coriacea.—Duellman, 1968, *Herpetologica*, 24:205.

Material.—Lago Agrio, 1; Santa Cecilia, 3.

Identification.—This moderately large frog with smooth, thick, glandular skin differs from all other species in the area by having a large, rectangular, dorsal blotch narrowly outlined by cream and red webbing. The only other species having red webbing is the much smaller *Hyla triangulum*, which has extensive axillary membranes and thin skin. Other

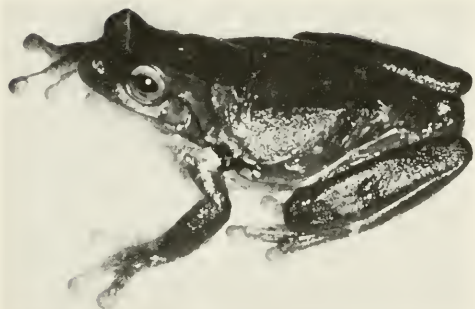


FIG. 100.—*Phrynohyas coriacea*, ♀, 64 mm SVL (KU 126656).

large brown hyalids having dark brown dorsal markings lack red webbing.

The snout is round, and the head is flat, slightly wider than long. A heavy dermal fold covers the upper edge of the tympanum, which is about three-fourths of the diameter of the eye. The skin on the dorsum is thick and smooth; that on the flanks and venter is granular. The fingers are about half webbed, and the toes are three-fourths webbed. The dorsum is tan (night) or reddish brown (day) with a large rectangular dark brown mark extending from the eyelids to the middle of the back, a dark brown blotch on the rump, and dark brown transverse bars on the limbs. All markings have a narrow creamy white border. The anterior and posterior surfaces of the thighs, ventral surfaces of the shanks, inner surfaces of the feet, and the webbing on the hands and feet are tomato red. The throat and belly are cream. A large bluish black or purple spot is present above the insertion of the arm. The iris is dark bronze to copper. Breeding males have a brown nuptial excrecence. ♂ 63 mm; ♀ 66 mm.

Occurrence.—Ecological data accompany only three specimens, all of which were taken at night. One was on a recently felled tree in primary forest; one was on the ground in secondary forest, and one was on a limb of a bush at the edge of the forest. Two were obtained in May and one each in July and October.

Life History.—No observations are available. The single female from May contained 1430 ovarian eggs. Presumably *P. coriacea*, like other members of the genus, deposits eggs in a film on the surface of ponds.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call is unknown.

Food.—The stomachs of two individuals contained a roach, orthopteran, ant, beetle, and spider.

Phrynohyas venulosa (Laurenti)

(FIGURE 101)

Rana venulosa Laurenti, 1768, Specimen medicum. . . Reptilium:31 [Type locality.—based on Plate 72, fig. 4 in Seba, 1734].

Phrynohyas venulosa—Hemming, 1958, Opin. Declar. Intl. Comm. Zool. Nomencl., 19: 172. Duellman, 1971, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 4:11.

Material.—Lago Agrio, 1.

Identification.—This large tree frog has thick, glandular, dorsal skin, usually bearing many large, low tubercles. The dorsum is gray, tan, or brown, usually with darker markings. The species is most easily confused with *Osteocephalus taurinus*, which differs by having thin skin and a pair of frontoparietal ridges. *Phrynohyas venulosa* differs from *P. coriacea* by lacking red thighs and webbing.

The snout is bluntly rounded, and the head is nearly as wide as long. The skin on the dorsum is thick, glandular, and usually tuberculate. A heavy dermal fold covers the upper part of the tympanum, which is about three-fourths of the diameter of the eye. The fingers are about one-third, and the toes two-thirds, webbed. The single specimen from Lago Agrio had a greenish gray dorsum with irregular brown marks on the back, brown transverse bars on the limbs, and dark brown spots on the flanks. The venter was greenish cream, and the iris was bronze with radiating black streaks. ♂ 75 mm.

Occurrence.—The single specimen

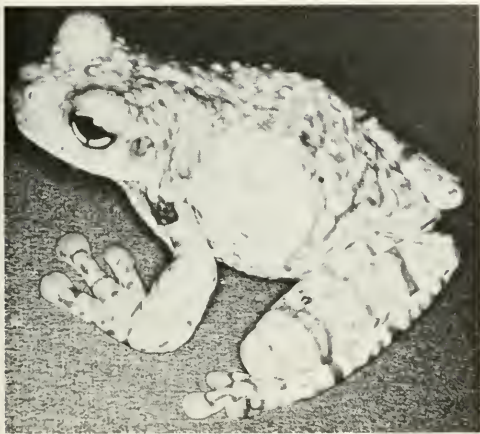


FIG. 101.—*Phrynohyas venulosa*, ♂, 75 mm SVL (KU 126657).

was obtained from a felled tree in primary forest.

Life History.—No observations were made in Ecuador, but data obtained on this species elsewhere in the Amazon Basin (Leticia, Colombia, and Belém, Brasil) and in Central America probably pertain to Ecuadorian populations. Breeding usually occurs only after torrential rains. Males call from the water or from bushes and trees around ponds. The eggs are deposited in a film on the surface of temporary ponds.

Tadpoles.—The following description is based on a tadpole (KU 124955) in stage 38 having a body length of 17 mm and a total length of 49 mm from Leticia, Colombia. The body is ovoid, as wide as deep, and deepest posteriorly. The snout is bluntly rounded. The eyes are moderately large and directed laterally. The nostrils are directed anterolaterally at a point midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point below the midline at about the midlength of the body. The anal tube is short and sinistral. The caudal musculature is moderately slender and attenuate. The fins are deeper than the musculature and are deepest at about two-fifths of the length of the tail. The dorsal and ventral fins are equal in depth,

and the dorsal fin extends onto the body. The tail is about 65 percent of the total length. The mouth is moderately small and directed anteroventrally. The median part of the upper lip is bare; elsewhere the lips are bordered by two rows of small labial papillae, except that papillae are more numerous in the lateral folds. The beaks are slender and bear fine serrations. The upper beak is in the form of a broad arch, and the lower beak is broadly V-shaped. There are three upper and six lower rows of denticles; the first upper row is broadly interrupted medially, and the last lower row is much shorter than the others. The body is brown above with a few scattered dark flecks; the belly is dull white. The caudal musculature is cream with dark brown stripes. The fins are translucent with a bluish gray tint posteriorly and brown flecks and reticulations on the dorsal fin. The iris is reddish bronze.

Tadpoles were in a pond in a clearing in rainforest near Leticia, Colombia. They oriented head-up, with the axis of the body at about 60° from the surface. The snouts were just below the surface. When disturbed they took refuge in debris on the bottom of the pond.

Mating Call.—The distinctive call of *P. venulosa* was not heard at Santa Cecilia. The call is a loud growl. Duellman (1970b: 168) noted that analysis of recordings made in Panamá and Costa Rica showed that the averages for various parameters are: 47 notes per minute, 0.30 sec duration, 161 pulses per second, fundamental frequency of 159 Hz, and dominant frequency of 1622 Hz.

Food.—The single specimen contained no food, but examination of specimens from elsewhere indicates that a wide variety of moderately large arthropods is eaten.

Remarks.—Duellman (1971) noted that 12 of 13 specimens from Amazonian Ecuador had uniformly brown dorsal coloration, whereas the other individual (from Lago Agrio) had a pattern consisting of anterior and posterior dorsal

markings. Proportionately, plain individuals are most abundant in the upper Amazon Basin. The largest male from Amazonian Ecuador is 92 mm, and the largest female is 110 mm.

Phyllomedusa palliata Peters

(FIGURE 102)

Phyllomedusa palliata Peters, 1872, Monatsb. Akad. Wiss. Berlin, 1872:773 [Type locality.—"Ucayali" (? = Río Ucayali), Departamento Loreto, Perú]. Duellman, 1974, *Herpetologica*, 30:107.

Material.—Durenó, 1; Santa Cecilia, 94+5.

Identification.—This small *Phyllomedusa* differs from its congeners by having small digital discs, and the sides of the head and flanks cream with brown flecks. All other green frogs in the area have the sides of the head green. Only *P. tomopterna* has patterned flanks (orange with vertical brown bars); it differs further from *P. palliata* by having moderately large discs and large calcears (absent in *P. palliata*).

The snout is rounded above and in males truncate below, in females inclined anteroventrally below. The parotoid glands are low, rounded, and extend only to the shoulder. The skin on the dorsum is smooth. The discs are small; webbing is absent, and the first toe is much longer than and opposable to the second. Calcears are absent. The dorsum and the sides of the head above the nostrils and middle of the orbits are dark green. The lower sides of the head and the flanks are cream with brown flecks. The groin and hidden surfaces of the limbs are orange with irregular brown marks. The venter is cream with brown flecks. The iris is bronze with fine black reticulations. Breeding males have brown nuptial excrescences. ♂ 45 mm; ♀ 50 mm.

Occurrence.—Individuals were about equally abundant in primary and secondary forest and in forest-edge habitats, where they usually were associated with temporary or permanent ponds. At most breeding sites the frogs were most com-



FIG. 102.—*Phyllomedusa palliata*, ♂, 44 mm SVL (KU 126661).

mon in low (< 1 m) herbaceous growth above the water. Individuals were observed in March through August and in October and December.

Life History.—Breeding occurs sporadically throughout the year. Males call from low, emergent vegetation in ponds in and at the edge of the forest. Eggs are deposited on the upper edges of leaves, usually in a tear-drop shape off of the tip of the leaf. Six clutches contained 38-71 ($\bar{X}=49.3$) unpigmented eggs having diameters of 3.5-4.0 ($\bar{X}=3.6$) mm. Fifteen gravid females contained 38-106 ($\bar{X}=60.8$) mature ovarian eggs. Apparently the entire ovarian complement is not necessarily deposited in one clutch. Five metamorphosing young have snout-vent lengths of 20-21 ($\bar{X}=20.4$) mm.

Tadpoles.—The following description is based on tadpoles (KU 124214) in stage 37 having a body length of 15 mm and a total length of 48 mm. The body is elongately ovoid, slightly deeper than wide, deepest at midlength of the body. The snout is truncate. The eyes are large, widely separated, and directed laterally. The nostrils are dorsal and directed anteriorly at a point about one-third of the distance from the tip of the snout to the eyes. The spiracular opening is directed posteriorly just left of the midline at a point at about the midlength of the body. The anal tube is short and dextral. The caudal musculature is ro-

bust proximally and gradually diminishes to a filamentous tip. The fins are shallow; the ventral fin is deepest, and at the midlength of the tail it is equal to two-thirds of the depth of the musculature. The fins do not extend to the tip of the tail, nor does the dorsal fin extend onto the body. The tail is about 70 percent of the total length. The small mouth is terminal; the upper lip is bare, whereas there is one row of small labial papillae laterally and two rows ventrally. There is no lateral fold. The beaks are moderately robust and bear small serrations. The upper beak is in the form of a highly curved arch, and the lower beak is V-shaped. There are two upper and three lower rows of denticles, of which the second upper row is broadly interrupted medially. The body and tail are bluish gray with an iridescent bluish green tint on the belly.

The tadpoles occur in open ponds where they orient head-up at an angle of about 45° to the surface. Usually they are found singly or in groups of less than 10. Upon being disturbed they seek refuge amidst vegetation or detritus on the bottom.

Mating Call.—The call is a soft “click” repeated at intervals of several seconds to three minutes. Analysis of two recordings made at Santa Cecilia reveals that the notes have a duration of 0.13–0.14 ($\bar{x}=0.135$) sec and 180–200 ($\bar{x}=190$) pulses per second. The fundamental frequency is at about 1500 Hz and the dominant frequency at 3000 Hz.

Food.—In 20 stomachs orthopterans and homopterans were the most frequently taken prey (40% and 35% of the stomachs, respectively). Spiders were present in one-fourth of the stomachs, whereas each of three frogs had eaten a fly, a beetle, and a caterpillar.

Remarks.—Although *P. palliata* and *P. tarsius* commonly were found at the same breeding sites at the same time, observations at one site throughout one year revealed that gravid females of only one species were present on a given



FIG. 103.—*Phyllomedusa tarsius*, ♂, 88 mm SVL (KU 123193).

night. The presence of one or the other was sporadic, not seasonal.

Phyllomedusa tarsius (Cope)

(FIGURE 103)

Pithecopus tarsius Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:113 [Type locality.—Río Amazonas, below mouth of Río Napo, Departamento Loreto, Ecuador].

Phyllomedusa tarsius—Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.: 428. Duellman, 1974, Herpetologica, 30:108.

Material.—Dureno, 1; Santa Cecilia, 105+8.

Identification.—This large species of *Phyllomedusa* differs from other members of the genus by having rounded parotoid glands extending to the mid-body or sacrum, the flanks marked by cream, pink, or pale orange spots, and an orange iris with black reticulations. The species is most easily confused with *P. vaillanti*, which has angular parotoid glands bearing a dorsolateral row of white tubercles, flanks that are green above and red below a row of longitudinally elliptical pale spots, and a pale gray iris. Other *Phyllomedusa* have orange or cream flanks with brown markings, and green frogs in other genera in the area have webbing and the first toe shorter than the second (webbing absent and first longer than second in *P. tarsius*).

The snout is inclined anteroventrally in both sexes and is angular above in males and round in females. The paro-

toid glands are rounded and extend to the midbody or sacrum. The skin on the dorsum is shagreened; that on the hind limbs is tuberculate in large individuals. The discs are moderately large; webbing is absent, and the first toe is longer than, and opposable to, the second. Calcareous are absent. The dorsal surfaces and sides of the head are green. The flanks are dull green or bluish green with discreet or confluent cream, pink, or pale orange spots. The anterior and posterior surfaces of the thighs are brown or dull green with cream, pale orange, or bluish-gray spots. The throat, chest, and ventral surfaces of the limbs are dark brown or grayish-brown; the belly is gray or pale orange-brown. Ventral markings consist of a pair of white spots on the throat, a median white spot on the chest, and usually a pair of para-anal white spots. The iris is bright orange with bold black reticulations. Breeding males have grayish brown nuptial excrescences. ♂ 97 mm; ♀ 111 mm.

Occurrence.—*Phyllomedusa tarsius* was found in March through October, with most individuals being observed in April through June. All were found in forest at night. Non-breeding individuals usually are perched on limbs 2-6 m above the ground.

Life History.—This species sporadically breeds after rains. Males have been heard calling from limbs of trees and bushes over ponds at various times throughout the year. Several hundred of these large frogs congregated at a forest pond bordered by spiny palms on the night of 2 April 1972. As many as four individuals were observed on one palm frond. Two nights later only a few individuals were found. The unpigmented eggs are deposited on or between leaves over ponds. Usually the frogs fold leaves over the clutch so as to conceal the eggs. Eight clutches contained 426-650 ($\bar{X}=551$) eggs having diameters of 3.5-4.0 ($\bar{X}=3.7$) mm. These clutches hatched in 7.0-8.3 ($\bar{X}=7.4$) days; hatchlings had total lengths of 11.5-13.0 ($\bar{X}=12.6$) mm.

Fifteen females contained 410-750 ($\bar{X}=549$) mature ovarian eggs; thus it seems as though this species usually deposits the entire ovarian complement as a single clutch. Fourteen metamorphosing young snout-vent lengths of 20-29 ($\bar{X}=25.3$) mm.

Tadpoles.—The following description is based on tadpoles (KU 153260) in state 36 having a body length of 18 mm and a total length of 50 mm. The body is ovoid, as wide as deep and deepest posteriorly. The snout is truncate. The eyes are large, widely separated, and directed laterally. The nostrils are directed anteriorly nearly at the tip of the snout. The opening of the sinistral spiracle is directed posteriorly nearly on the midline and at a point at about midlength of the body. The dextral anal tube is short. The caudal musculature is robust proximally, gradually tapering to a terminal point. A shallow dorsal fin is present only on the posterior two-thirds of the tail. The ventral fin is shallower than the musculature and extends to the tip. The tail is about 64 percent of the total length. The small terminal mouth lacks lateral folds. The upper lip is bare; there is one row of small labial papillae laterally and two rows ventrally. The beaks are moderately robust with coarse serrations. The upper beak is a narrow arch, and the lower beak is V-shaped. There are two upper and three lower rows of denticles; the second upper row is broadly interrupted medially. The dorsal surfaces of the body and tail are pale tan; the sides and venter are pale metallic green. The iris is bronze.

Tadpoles orient head-up at an angle of about 45° to the surface of the water. Although some have been found singly or in small numbers, two large concentrations were found in open water. Each congregation consisted of at least 100 individuals; all were oriented in the same way.

Mating Call.—The call is a moderately loud low-pitched "cluck." Analysis of three recordings from Santa Cecilia

provides the following data: 2.0-3.2 ($\bar{X}$ =2.7) notes per minute, 80 pulses per second; and notes having a duration of 0.5-0.7 ($\bar{X}$ =0.58) sec. The fundamental frequency at 304-522 ($\bar{X}$ =375) Hz is dominant.

Food.—Twenty of 21 stomachs examined contained only Orthoptera, most of which were large and only one to a stomach. The largest orthopteran was 43 mm in length. The other stomach contained a spider.

Taxonomic Comments.—Most references to the large *Phyllomedusa* in Amazonian Ecuador have been under the specific names *P. edentula* Andersson or *P. orcesi* Funkhouser; Duellman (1974b) showed that those names were junior synonyms of *P. tarsius* (Cope), a species widespread in the upper Amazon Basin in Colombia, Ecuador, and Perú.

Remarks.—The exclusive occurrence of gravid females of *P. tarsius* and *P. palliata* is discussed in the account of *P. palliata*.

Phyllomedusa tomopterna (Cope)

(FIGURE 104)

Pithecopus tomopternus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:112 [Type locality.—Río Amazonas, below the mouth of Río Napo, Departamento Loreto, Perú].

Phyllomedusa tomopterna—Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.:430. Duellman, 1974, Herpetologica, 30:109.

Material.—Lago Agrio, 1+1; Santa Cecilia, 61+2.

Identification.—*Phyllomedusa tomopterna* is readily distinguished by its coloration—bright green dorsum, and flanks and hidden surfaces of the thighs orange with purplish brown vertical bars. The only other green frog in the area having brown markings on the flanks and thighs is *P. palliata*, which differs from *P. tomopterna* in having the sides of the head and the flanks cream with brown flecks, smaller digital discs, and no calcars.

The snout is truncate in males and rounded in females. The parotoid glands are diffuse and usually not evident. The

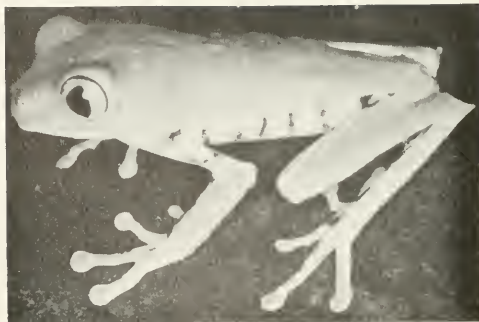


FIG. 104.—*Phyllomedusa tomopterna*, ♂, 42 mm SVL (KU 139257).

skin on the dorsum is smooth. The discs are large; webbing is absent, and the first toe is barely longer than and opposable to the second. Large calcars are present. The dorsal surfaces and sides of the head are green. The flanks and hidden surfaces of the limbs are orange with vertical purplish brown bars. The throat and chest are white, and the belly is pale orange. The iris is silvery gray. Breeding males have brown nuptial excrescences. ♂ 48 mm; ♀ 57 mm.

Occurrence.—All individuals of this species were found at night on bushes and low trees in forest from March through November.

Life History.—Although *P. tomopterna* has an extensive breeding season, it is doubtful if it breeds throughout the year. Data are lacking for January, February, and December, usually the driest months at Santa Cecilia. Males call from bushes and trees over ponds. Five gravid females from April and July contained 60-89 ($\bar{X}$ =71.4) unpigmented ovarian eggs 3.5 mm in diameter; no clutches were found.

Tadpoles.—The following description is based on a tadpole (KU 152320) in stage 38 having a body length of 23 mm and a total length of 64 mm. The body is elongately ovoid, as wide as deep and deepest posteriorly. The snout is truncate. The large eyes are widely separated and directed laterally. The nostrils are dorsal and directed anteriorly at a point

one-third the distance from the tip of the snout to the eyes. The opening of the sinistral spiracle is just off the midline and directed posteriorly at about the midlength of the body. The anal tube is short and dextral. The caudal musculature is robust proximally and gradually diminishes to a terminal filament. The dorsal fin is very low; the ventral fin is slightly shallower than the musculature and extends to the tip of the tail. The tail is about 65 percent of the total length. The small terminal mouth lacks lateral folds. The upper lip is bare; elsewhere the lips are bordered by two rows of small labial papillae. The beaks are moderately robust and bear fine serrations. The upper beak forms a broad arch, and the lower beak is in the form of a flared V. There are two upper and three lower rows of denticles; the second upper row is broadly interrupted medially. The body and tail are yellow or yellowish tan; the belly is white. A diffuse orange spot is present on the posterior part of the ventral fin. The iris is silvery white.

Mating Call.—The call is a soft “cluck.”

Food.—Three of six stomachs contained a roach each, and the other three each contained an orthopteran, one of the latter also had an homopteran.

Remarks.—*Phyllomedusa tomopterna*, despite its gaudy appearance, is the least conspicuous *Phyllomedusa* in the area. It seems to prefer more dense vegetation than the other species. Half of our specimens were obtained from a palm-shrouded pond on 2 and 4 April 1972.

Phyllomedusa vaillanti Boulenger

(FIGURE 105)

Phyllomedusa vaillanti Boulenger, 1882, Cat. Batr. Sal. Brit. Mus.:427 [Type locality.—Santarém, Estado do Pará, Brasil]. Duellman, 1974, *Herpetologica*, 30:109.

Material.—Dureno, 1; Puerto Libre, 1; Santa Cecilia, 64+2.

Identification.—*Phyllomedusa vail-*



FIG. 105.—*Phyllomedusa vaillanti*, ♀, 49 mm SVL (KU 139252).

lanti is a large green tree frog without webbing and characterized by angular parotoid glands bearing a dorsolateral row of small white tubercles. It is most similar to *P. tarsius*, which has round parotoid glands and no white tubercles, and an orange iris with black reticulations (pale gray in *P. vaillanti*). Other *Phyllomedusa* in the area have cream or orange flanks with brown markings; in *P. vaillanti* the flanks are green above and red below a row of pale spots.

The snout is angular above and nearly truncate in males, rounded above and inclined anteroventrally in females. The parotoid glands are slightly elevated, angular, and extend to the sacrum; there is a longitudinal row of white granules along the angle of the gland. The skin on the dorsum is rough; it is tubercular on the hind limbs in large individuals. The discs are moderately large; webbing is absent, and the first toe is longer than, and opposable to, the second. Calcears are absent. The dorsum and side of the head are green; the flanks are green above and reddish brown below a row of longitudinally elliptical cream to pale orange spots. The anterior and posterior surfaces of the thighs are reddish brown or lavender with small cream to pale

orange spots. The venter is dull grayish brown with a pair of lavender-bordered cream spots on the throat and a pale green spot on the chest. The iris is pale gray with a greenish tint. Breeding males have grayish brown nuptial excrescences. ♂ 58 mm; ♀ 84 mm.

Occurrence.—Individuals of this species were found in primary and secondary forest at night in all months, except November and December. Adults were on bushes and trees to heights of 4 cm.

Life History.—Males call from bushes over ponds, but no breeding congregations were encountered. Five gravid females from March, April, June, and August contained 912-1250 ($\bar{X}$ =1114) mature ovarian eggs having diameters of 2.0 mm. One female deposited a clutch of 645 unpigmented eggs 2.0 mm in diameter. The eggs are deposited on vegetation above ponds. Eleven metamorphosing young from February (2), June (1), and July (8) have snout-vent lengths of 21-25 ($\bar{X}$ =23.8) mm.

Tadpoles.—The following description is based on a tadpole (KU 152319) in stage 38 having a body length of 19 mm and a total length of 52 mm. The body is elongately ovoid, slightly deeper than wide. The snout is truncate. The large eyes are widely separated and directed laterally. The nostrils are directed anteriorly nearly at the tip of the snout. The spiracular opening is directed posteriorly just to the left of the midline at a point at about the midlength of the body. The anal tube is short and dextral. The caudal musculature is robust proximally and gradually narrows to a slender tip. The dorsal fin is very shallow, and the ventral fin is shallower than the musculature and extends to the tip of the tail, which is about 63 percent of the total length. The small terminal mouth lacks lateral folds. The upper lip is bare; elsewhere the mouth is bordered by two rows of small labial papillae. The beaks are moderately robust with fine serrations. The upper beak is a broad arch with slender alary processes; the lower

beak is broadly V-shaped. There are two upper and three lower rows of denticles; the second upper row is broadly interrupted medially. The dorsum is olive green, paler on tail than on body. The belly is white, and the ventrolateral surfaces are iridescent yellowish green. The iris is pale bronze.

Mating Call.—The call consists of a short, harsh, "cluck." Analysis of one recording from Pilcopata, Departamento Cuzco, Perú, shows 13.3 notes per minute having a duration of 0.5 sec, 240 pulses per second, and a dominant frequency at about 1800 Hz.

Food.—Sixteen of 18 stomachs contained orthopterans up to 34 mm in length. The other two contained spiders.

Taxonomic Comments.—Most references to this species in the upper Amazon Basin have been under the name of *Phyllomedusa perlata*, a name synonymized with *P. vaillanti* by Duellman (1974b).

Remarks.—*Phyllomedusa vaillanti* apparently breeds at sites exclusive of those used by the other three species of *Phyllomedusa*. At two ponds where the other species called commonly at various times throughout the year, *P. vaillanti* was never found. Instead individuals of *P. vaillanti* were scattered throughout the forest or in small groups at temporary ponds.

Sphaenorhynchus carneus (Cope)

(FIGURE 106)

Hylella carnea Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 1868:111 [Type locality.—

"Napo or upper Marañon" (? Perú)].

Sphaenorhynchus carneus—Duellman, 1974, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 27:22.

Material.—Santa Cecilia, 19.

Identification.—This small green tree frog with a protruding snout has cream (night) or red (day) canthal and dorso-lateral stripes. This color pattern resembles that of the larger *Hyla punctata* which has a round, non-protruding snout and less webbing on the feet. The much



FIG. 106.—*Sphaenorhynchus carneus*, ♂, 19 mm SVL (KU 146576).

larger *Sphaenorhynchus eurhostus* also has a protruding, acuminate snout, but it lacks red dorsolateral stripes and has more webbing on the hand. All other small green frogs in the area have rounded snouts, except *Eleutherodactylus acuminatus*, which differs from *S. carneus* in lacking webbing and a tympanum.

The snout is narrowly truncate in dorsal view, acuminate and protruding well beyond the jaw in profile. The anterior edge of the tympanum is evident. The skin of the dorsum is smooth; that on the venter is weakly granular. The fingers are about one-third webbed and the toes three-fourths webbed. At night the dorsum is pale green with golden cream canthal and dorsolateral stripes. By day the dorsum is dark green with reddish brown flecks and faint greenish cream canthal and dorsolateral stripes bordered below by reddish brown stripes. The belly is white, and other ventral surfaces are pale green. The axilla and groin are blue, and the webbing is unpigmented. The iris is pale silver, and the bones are green. Breeding males have brown nuptial excrescences. ♂ 20 mm; ♀ 23 mm.

Occurrence.—All individuals were on emergent vegetation in a pond in primary forest; they were observed there on five nights in April and May, 1972, and on one night in June 1975.

Life History.—Males call from emergent vegetation. One female contained 143 mature ovarian eggs. No other data on life history are available.

Mating Call.—The call is a series of loud clicks. Analysis of three recordings from Santa Cecilia revealed that notes are produced at a rate of 23-180 ($\bar{X}=77$) notes per minute. The duration of the notes is 0.02-0.05 ($\bar{X}=0.025$) sec, and the pulse rate is 180 pulses per second. The dominant frequency is 4750-5000 ($\bar{X}=4880$) Hz.

Food.—Six individuals contained only ants.

Sphaenorhynchus eurhostus Rivero (FIGURE 107)

Sphaenorhynchus eurhostus Rivero, 1969, *Copeia* (1969(4):701 [Type locality.—“? Brasil”]).

Material.—Santa Cecilia, 1.

Identification.—This moderate-sized green tree frog has an acuminate snout protruding well beyond the margin of the jaw. Only the much smaller *Sphaenorhynchus carneus* has a protruding snout, but that species has cream dorsolateral stripes and less webbing on the hand. Other green frogs in the area have rounded, truncate, or acuminate snouts that do not protrude beyond the margin of the jaw; furthermore, all have less webbing on the hand than does *S. eurhostus*.

The snout is acuminate in dorsal view and pointed and protruding well anterior to the margin of the lip in profile. The tympanum is barely evident. The fingers are half and the toes four-fifths webbed. The skin on the dorsum is smooth; that on the belly is weakly granular. The dorsum is green; the belly, ulnar, tarsal, and anal stripes are creamy white, and the canthal stripe is dark brown. The ventral surfaces of the limbs are bluish green, and the iris is pale creamy bronze.



FIG. 107.—*Sphaenorhynchus eurhostus*, juvenile, 21 mm SVL; Belém, Estado do Pará, Brasil (KU 127981).



FIG. 108.—*Centrolenella midas*, ♂, 20 mm SVL (KU 123219).

Breeding males have brown nuptial excrescences. ♀ 48 mm.

Occurrence.—The single specimen from Santa Cecilia was on a bush at the edge of primary forest at night in August.

Life History.—The single female contained 550 mature ovarian eggs. Observations on this species in Brasil and Venezuela indicate that the males call on vegetation overhanging ponds at the edge of forest. Presumably the eggs are deposited in ponds.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call consists of a short, low pitched note, folowed or not by a secondary note. Analysis of two recordings from Georgetown, Guyana, reveals that notes are produced at a rate of 20-24 ($\bar{X}=22$) notes per minute. The notes have a duration of 0.05-0.10 ($\bar{X}=0.07$) of a second and a rate of 200-240 ($\bar{X}=217$) pulses per second. The fundamental frequency is at 350-410 ($\bar{X}=391$) Hz and the dominant frequency at 1050-1230 ($\bar{X}=1183$) Hz.

Food.—The single individual contained two ants.

Remarks.—A male from Limoncocha, Ecuador, has a snout-vent length of 41 mm.

CENTROLENIDAE

Centrolenella midas Lynch and Duellman

(FIGURE 108)

Centrolenella midas Lynch and Duellman, 1973, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 16:38 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 2; Puerto Libre, 4; Santa Cecilia, 7+1.

Identification.—This small centrolenid differs from the other species by having a dark green dorsum with scattered gold flecks dorsolaterally on the body. It further differs from *C. resplendens* by lacking lateral dermal fringes on the forearms and feet and by having a truncate instead of a sloping snout. *Centrolenella midas* also differs from *C. munozorum* in snout shape (round in *C. munozorum*) and in having the lower two-thirds of the tympanum visible (tympanum entirely concealed in *C. munozorum*). *Centrolenella midas* differs from *Hyla granosa* in snout shape, dorsal coloration, and smaller size; *H. granosa* has a round snout and uniform green dorsum, in addition to having rounded discs on the fingers (truncate in *Centrolenella*). The shape of the discs also distinguishes *C. midas* from species of *Sphaenorhynchus*, which have a pointed snout protruding anteriorly beyond the margin of the lip. The green *Eleutherodactylus acuminatus* has no webbing on the hand and has a black canthal stripe.

The dorsal surfaces of the head, body, and limbs are dark green with a few small golden yellow flecks dorsolaterally

on the body (in preservative lavender with white flecks). The hands and feet are dull greenish yellow. The chest is white, and the heart is not visible; the visceral peritoneum is white. The bones are green, and the iris is silvery bronze with black reticulations. ♂ 19 mm; ♀ 26 mm.

Occurrence.—Two were obtained from tree tops as trees were felled by day. Others were found on low vegetation at night in both primary and secondary forest. The specimens from Puerto Libre and three of those from Santa Cecilia were on bushes and herbs adjacent to, or overhanging, small shallow streams. Individuals were found in April-August and November.

Life History.—Two females (April and August) show no evidence of reproductive activity, and two others (April and May) have small ovarian eggs. Four females (June, July 2, November) have 14-29 ($\bar{X}=22$) large ovarian eggs. A tadpole tentatively referred to this species was found in June.

Tadpoles.—A single centrolenid tadpole was found in the shallow stream at Santa Cecilia where numerous *Centrolenella midas* were heard and a few collected. No other centrolenids were found along the stream, so the tadpole (KU 124218) is tentatively referred to *C. midas*. The tadpole is in developmental stage 25 and has a body length of 6.2 mm and a total length of 19.0 mm. The body is elongate and depressed; the eyes are small, close together, and directed dorso-laterally. The mouth is directed antero-ventrally and is bordered laterally and ventrally by one row of small papillae. The beaks are robust and serrate. One upper and two lower rows of denticles are present. The caudal fins are low; only on the posterior one-third of the tail are the fins deeper than the robust caudal musculature. The tadpole essentially lacks pigment in the skin.

Mating Call.—The call is a high-pitched triple note "peep-peep-peep" re-



FIG. 109.—*Centrolenella munozorum*, ♀, 23 mm SVL (KU 123225).

peated at intervals of more than 20 seconds.

Food.—Two individuals contained food — one spider and one homopteran.

Centrolenella munozorum

Lynch and Duellman

(FIGURE 109)

Centrolenella munozorum Lynch and Duellman, 1973, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 16:40 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Lago Agrio, 1; Santa Cecilia, 12+1.

Identification.—This small centrolenid differs from the other species by having white bones and a clear parietal peritoneum resulting in the heart being visible through the ventral skin. Furthermore, it differs by having a round snout (truncate in *C. midas* and sloping in *C. resplendens*). *Centrolenella munozorum* has a pale green dorsum with large, diffuse yellow spots, contrasting with many small white spots in *C. resplendens* and few small gold flecks in *C. midas*. *Centrolenella munozorum* further differs from *C. resplendens* by lacking lateral dermal fringes on the forearms and feet. Hylids (*Sphaenorhynchus* and *Hyla granosa*) differ by having rounded, instead of truncate, discs on the fingers and either uniformly green dorsal surfaces or red dorsolateral stripes). The only green *Eleutherodactylus* (*E. acuminatus*) lacks

webbing on the hand and has a black canthal stripe.

The dorsum is pale green with diffuse pale yellow or greenish yellow spots (in preservative, creamy white with minute black flecks). The limbs are pale green, except for the thighs, which are unpigmented. The iris is pale gold. ♂ 20 mm; ♀ 21 mm.

Occurrence.—One was obtained from the canopy of a large tree felled in primary forest. Others were found on vegetation in or near swamps in primary or secondary forest at night and along small trickling streams at the edge of the forest. Individuals were found in April through October.

Life History.—A female (July) contained 18 large ovarian eggs. Males were calling from low vegetation over a rivulet in September and October; tadpoles were found in the stream in October.

Tadpoles.—The following description is based on tadpoles (KU 155524) in stage 25 having a body length of 4.2 mm and a total length of 13 mm. The body is elongately and narrowly ovoid, wider than deep. The snout is bluntly rounded. The eyes are small and directed dorso-laterally. The nostrils are directed anterodorsally about midway between the snout and the eyes. The opening of the sinistral spiracle is directed posterodorsally at a point just below the midline at about midbody. The anal tube is long and dextral. The caudal musculature is robust, forming more than half of the depth of the tail. The fins are about equal in depth to one another, except that the dorsal fin is very low anteriorly and does not extend onto the body. The tip of the tail is rounded. The tail is about 70 percent of the total length. The mouth is small, directed anteroventrally, and bordered laterally and ventrally by one row of small papillae. The beaks are moderately robust and finely serrate. There are two rows of denticles below the beaks and none above. Except for a few dark flecks on the dorsal edge of the caudal musculature, pigment is lacking.



FIG. 110.—*Centrolenella resplendens*, ♂, 27 mm SVL (KU 118053).

Mating Call.—The call is a soft, high-pitched, single note.

Food.—One individual contained a spider, and two contained small beetles.

Centrolenella resplendens

Lynch and Duellman

(FIGURE 110)

Centrolenella resplendens Lynch and Duellman, 1973, Occas. Papers Mus. Nat. Hist. Univ. Kansas, 16:51 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Santa Cecilia, 1.

Identification.—This, the largest centrolenid in the area, differs from all other frogs there by having a dark green dorsum with many white tubercles, a long sloping snout, a U-shaped anal fold, and a scalloped dermal fold along the outer edge of the hand, forearm, and elbow, and another along the outer edge of the heel, tarsus, and foot. Other centrolenids and green hylids and *Eleutherodactylus* have smooth skin on the dorsum, lack scalloped dermal folds on the limbs, and have round or truncate snouts. The only other frog in the area having scalloped folds on the limbs is the larger *Hyla marmorata*, which is mottled gray, green, and brown above and black, white, and yellow below.

The dorsum is dark green with small white to pale bluish green spots on tubercles; the fringes on the limbs and around the anus are white. The venter is yellow, and the iris is gray. ♂ 27 mm.

Occurrence.—The only known specimen from Santa Cecilia was on the leaf of a bush about 30 cm above the ground in primary forest. It was found during a light rain on the night of 14 June 1967.

Life History.—Nothing is known; presumably the species deposits its eggs on vegetation overhanging streams like centrolenids. A juvenile having a snout-vent length of 16.5 mm was found in October at Santa María de Sucumbios, Colombia (40 km NNW of Santa Cecilia).

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call is unknown.

Food.—The only known adult, the holotype, was not examined for stomach contents.

RANIDAE

Rana palmipes Spix

(FIGURE 111)

Rana palmipes Spix, 1824, *Animalia nova . . . testudinum et ranarum . . . Brasilian*, p. 5 [Type locality.—"Amazonenfluss"]. Cochran and Goin, 1970. *Bull. U. S. Natl. Mus.*, 288:70.

Material.—Puerto Libre, 1; Santa Cecilia, 97+7.

Identification.—This large smooth-skinned frog with fully webbed toes and large tympanum is readily distinguished from all other frogs in the area. The species of *Leptodactylus* have much less, if any webbing on the feet and have a ventral abdominal disc (absent in *Rana*). The only other frog that might be confused with *Rana palmipes* is *Hyla lanciformis*, which differs by having large terminal discs on the fingers and toes.

The body is moderately robust, and the snout is acuminate in dorsal view and round in profile. The tympanum is nearly as large as the eye. The fingers are unwebbed and webbing extends to the terminal phalanges of all but the fourth toe. The dorsum varies from bright green to olive-green or olive-tan, usually always with a green snout. Some individuals have irregular dark brown

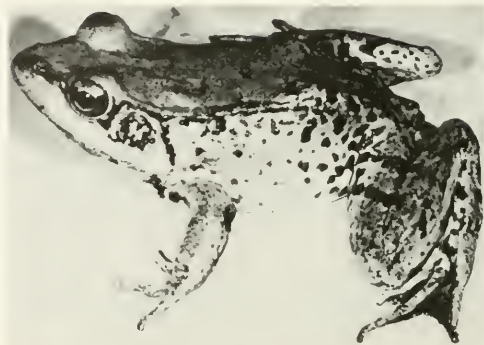


FIG. 111.—*Rana palmipes*, ♂, 89 mm SVL (KU 146639).

or black spots on the dorsum. The flanks are tan with dark brown or black spots. The venter is creamy yellow with a grayish suffusion on the throat and black flecks on the ventral surfaces of the limbs and on the posterior part of the belly. The posterior surfaces of the thighs are black with creamy yellow reticulations. The iris is reddish brown with a bright bronze cast dorsally. ♂ 101 mm; ♀ 126 mm.

Occurrence.—*Rana palmipes* is widely distributed in a variety of habitats, but 80 percent of the specimens were found within 3 m of water. Some juveniles were found under logs or in small streams by day, but adults were found only at night. Thirty-five percent of the frogs were in, or at the edge of, swamps or lakes, and 30 percent were in, or at the edge of streams, and 5 percent were on the bank of the river. The frogs were found in clearings and forest. Adults were found throughout the year.

Life History.—Males were heard calling throughout the year from lakes, swamps, streams, and the river. Gravid females were found throughout the year, except December and January, when no females were found. Twenty-five females having snout-vent lengths of 103-125 ($\bar{X}=117$) mm contained 720-6750 ($\bar{X}=2860$) ovarian eggs. Eggs are deposited in clumps in ponds or in quiet pools in streams. Two metamorphosing young

have snout-vent lengths of 48 and 53 mm.

Tadpoles.—The following description is based on a tadpole (KU 152332) in stage 35 having a body length of 37 mm and a total length of 92 mm. The body is ovoid, as wide as deep, and deepest posteriorly. The snout is bluntly rounded. The eyes are moderately large, widely separated, and directed laterally. The nostrils are directed anteriorly at a point about two-thirds of the distance from the eyes to the snout. The opening of the sinistral spiracle is directed posterolaterally well below the midline at a point about midlength of the body. The cloacal tube is short and medial. The caudal musculature is moderately robust, gradually tapering to the tip. The fins are subequal in depth and deepest at about midlength of the tail, where the depth of each is about equal to the depth of the caudal musculature. The fins terminate in a rounded tip, and the dorsal fin does not extend onto the body. The tail is about 60 percent of the total length. The mouth is small and directed anteroventrally. The median part of the upper lip is bare, and the median part of the lower lip bears a single row of small papillae; elsewhere there are two rows of papillae. The lips are folded laterally. The beaks are slender and bear fine serrations. The upper beak is a broad, flattened arch, and the lower beak is a broad curved arch depressed medially. There are two upper and four lower rows of denticles; the second upper and first lower rows are interrupted medially. A short lateral row is present on either side of the beak. The dorsum is greenish brown mottled with dark brown. The belly is cream with gray spots, and the tail is orange-tan. The iris is bronze.

Tadpoles are solitarily pelagic in quiet water.

Mating Call.—The call is a series of guttural chuckling sounds produced in water.

Food.—Examination of 17 stomachs

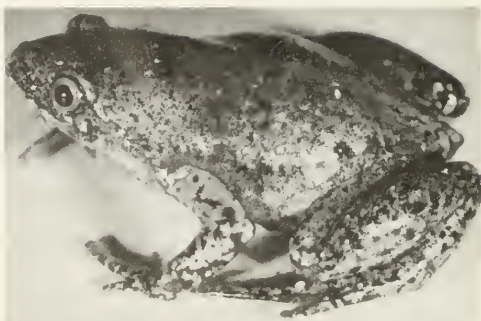


FIG. 112.—*Chiasmocleis anatipes*, ♂, 19 mm SVL (KU 146034).

revealed a variety of large prey, the largest being a mantid 63 mm long in a frog having a snout-vent length of 98 mm. Orthopterans (35% of stomachs), beetles (30%) and spiders (30%) were the most common prey items. Caterpillars were found in two stomachs and each of the following in one: dipteran, hymenopteran, homopteran, odonate, and odonate nymph.

MICROHYLIDAE

Chiasmocleis anatipes Walker and Duellman

(FIGURE 112)

Chiasmocleis anatipes Walker and Duellman, 1974; Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 26:1 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Santa Cecilia, 13+2.

Identification.—Among the microhylid frogs in the region, all of which have narrow snouts and small eyes, *C. anatipes* is the only species having nearly fully webbed feet. The much larger *Ctenophryne geayi* has toes less than one-half webbed, and the ventral surfaces are dark brown with cream flecks. In *C. anatipes* the venter is white with irregular large black spots, a pattern shared with *C. ventrimaculatus*, a species in which the toes have only basal webbing. *Chiasmocleis bassleri* and *Hamptophryne boliviana* have only basal webbing on the feet, dark throats, and mottled bellies. The only other microhylid in the

area, *Syncope antenori* has only four toes and a visible tympanum (tympanum concealed in others).

The body is relatively slender, and the snout tapers medially, anterior to the eyes, to a rounded tip. The limbs are slender. The fingers bear lateral fringes, and the toes are webbed to the bases or middle portions of the terminal discs. The skin is smooth above and below with scattered minute tubercles on the dorsal surfaces of the head, body, and hind limbs. The dorsum is dull olive-green to dull brown with green and/or gold metallic flecks; a narrow middorsal tan stripe is present in some specimens. The upper arms are tan or orange. The posterior surfaces of the thighs are gray with black flecks. The throat is pale gray with bold black mottling, and the belly and the ventral surfaces of the thighs are white with large, brownish black marks. The iris is reddish brown. Breeding males lack nuptial excrescences. ♂ 20 mm.

Occurrence.—All individuals were found in or near a semi-permanent pond in primary forest at night. In April 1972 the frogs were on the ground or on leaves of low (< 25 cm) herbs, but in May 1975 six males were calling from the shallow part of the pond.

Life History.—With the exception of the presence of calling males in May and tadpoles in April, no observations are available; females have not been found.

Tadpoles.—The following description is based on a tadpole (KU 146836) in stage 37 having a body length of 9.5 mm and a total length of 32.5 mm. The body is as deep as wide, widest anteriorly with a bluntly rounded snout. In profile the snout is round. The eyes are small and directed laterally. The spiracles are paired ventrolaterally; the cloacal tube is dextral. The caudal musculature is slender, tapering gradually to a pointed tip beyond the terminus of the fins, which are deepest at midlength of the tail and about twice the depth of the caudal musculature. The dorsal fin does

not extend onto the body. The tail comprises about 69 percent of the total length. The small, terminal mouth is directed anterodorsally and lacks papillae and keratinous structures. The body is olive-tan above and yellowish white below.

The tadpoles were swimming individually near the surface of the pond during the day.

Mating Call.—The call consists of a short buzz.

Food.—Only small ants had been eaten.

Remarks.—In addition to the seven specimens reported by Walker and Duellman (1974), six adult males obtained by Ronn Altig in 1975 have been examined. They agree in all respects with the type series.

Chiasmocleis bassleri Dunn

Chiasmocleis bassleri Dunn, 1949, Amer. Mus. Novitates, 1419:9 [Type locality.—Río Utoquinia to Río Tapiche, Departamento Loreto, Perú].

Material.—Lago Agrio, 1; Santa Cecilia, 7.

Identification.—Like most other microhylid frogs in the region, *C. bassleri* has a narrow snout, small eyes, and a concealed tympanum; the toes are only basally webbed, a character distinguishing *C. bassleri* from *C. anatipes* and *Ctenophryne geayi*, which have more extensive webbing. The throat and chest are brown with pale flecks, whereas the belly and ventral surfaces of the limbs are white with large black spots. In *C. ventrimaculata* the entire venter is white with black spots. The larger *Hamptophryne boliviana* has a ventral pattern like that of *C. bassleri*, except the spots are smaller and more numerous. Furthermore, the dorsum in *H. boliviana* is pale and sharply delineated by dark flanks, whereas in *C. bassleri* the dorsum is dark and not differentiated from the coloration of the flanks. *Chiasmocleis bassleri* has five toes and a concealed tympanum, characters distinguishing it

from *Syncope antenori*, which has four toes and a visible tympanum.

The body is robust, and the head tapers medially from the angle of the jaws to a pointed snout. The forelimbs are slender, and the hind limbs are moderately robust. The fingers lack lateral fringes, and the toes are barely webbed basally. The skin is smooth above and below. The dorsum and flanks are uniform grayish brown. The dorsal surfaces of the forelimbs are pinkish tan. There are indistinct pink spots on the flanks and anterior surfaces of the thighs. A pair of small black spots is present in the inguinal region. The throat and chest are gray; the belly and ventral surfaces of the hind limbs are white with large black or brownish black spots. The iris is greenish silver with dark brown reticulations. Breeding males lack nuptial excrescences. ♂ 22 mm; ♀ 28 mm.

Occurrence.—Individuals of this species were found in equal numbers in primary and secondary forest. With the exception of one individual on an herbaceous leaf 20 cm above the ground, all were found on the ground. The annual distribution is January (1), May (2), June (1), July (1), August (1), November (1), and December (1).

Life History.—No observations on breeding are available. Three females from June, July, and November contained 235, 250, and 151 mature ovarian eggs, respectively.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call is unknown; presumably it is a buzzing sound like that of other members of the genus.

Food.—Minute beetles were found in four stomachs and ants in four stomachs; also one individual had eaten two tiny wasps in addition to an ant.

Chiasmocleis ventrimaculata (Andersson)

Engystoma ventrimaculata Andersson, 1945,
Arkiv. Zool., 37A:2 [Type locality.—Río
Pastaza, Ecuador].

Chiasmocleis ventrimaculata—Dunn, 1949,
Amer. Mus. Novitates, 1419:8.

Material.—Santa Cecilia, 9.

Identification.—*Chiasmocleis ventrimaculata*, like other microhylid frogs in the area, has a narrow snout and small eyes. The dorsum is dark brown, and the entire venter is white with large irregular black spots—characters immediately distinguishing the species from *Chiasmocleis bassleri*, *Ctenophryne geayi*, and *Hamptophryne boliviana*, all of which have dark throats and chests with pale flecks. Furthermore, in *Hamptophryne* and *Ctenophryne* the dorsum is pale and sharply delineated from dark flanks. The ventral coloration of *C. ventrimaculata* is shared with *C. anatis*, which has nearly fully webbed feet; the toes are webbed basally in *C. ventrimaculata*. The only other microhylid frog in the area is *Syncope antenori*, a small species having four toes and a concealed tympanum.

The body is moderately slender, and the head tapers medially from the angle of the jaws to an acutely rounded tip. The limbs are slender. The fingers lack fringes, and the toes are barely webbed basally. The skin is smooth above and below. The dorsum is dark olive-brown with minute gold flecks. All ventral surfaces are bluish white with irregular bold black spots. The iris is reddish brown. Breeding males lack nuptial excrescences. ♂ 23 mm; ♀ 22 mm.

Occurrence.—All individuals were found at night in primary forest; some were on low herbs, others were on the ground, and one was calling from the edge of a shallow pond. The seven frogs were found in April (1), May (4), June (1), and July (1).

Life History.—A male was calling in May, and one female from June contained 210 mature ovarian eggs. Recently metamorphosed young were found in April and May.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call consists of a soft buzz.

Food.—Only small ants were found in three stomachs.

Ctenophryne geayi Mocquard

Ctenophryne geayi Mocquard, 1904, Bull. Mus. Hist. Nat. Paris, p. 308 [Type locality.—Río Sarare Departamento Norte de Santander, Colombia]. Dunn, 1949, Amer. Mus. Novitates, 1419:18.

Material.—Santa Cecilia, 4.

Identification.—This is the largest microhylid frog in the area, and it has a squat, robust body with a small pointed head. The toes are about four-fifths webbed, and the venter is dark with cream flecks—a combination of characters distinguishing *C. geayi* from all other microhylid frogs in the area. *Chiasmocleis anatipes* has the toes almost fully webbed; in that species and *Chiasmocleis ventrimaculata* the venter is white with black spots. In *Chiasmocleis bassleri* and *Hamptophryne boliviana* the throat and chest are dark with pale flecks, and the rest of the venter is white with dark spots. *Hamptophryne boliviana* and *C. geayi* are alike in having a pale dorsal color sharply delineated from dark flanks. In *C. geayi* the dorsal color is continuous onto the arm, whereas in *Hamptophryne* the pale color on the arm is separated from that on the body by the dark color of the flanks. The only other microhylid in the area is the minute *Synecope antenori*, which has only four toes and a visible tympanum; *C. geayi* has five toes and a concealed tympanum.

The body is robust, the head tapers medially from the angles of the jaws to a round snout. The limbs are moderately robust. Lateral fringes are present on the fingers, and the toes are webbed nearly to the bases of the terminal discs. The skin is smooth above and below. The dorsum is pale brown with a pale cream middorsal line and minute cream flecks. The dorsal color, which is continuous onto the arms, is delineated by a narrow creamy white line, separating the

dorsal color from the darker brown flanks and anterior and posterior surfaces of the thighs. The vocal sac is dark grayish brown; the other ventral surfaces are dark brown with white flecks. The iris is grayish bronze. Males lack nuptial excrescences. ♂ 32 mm; ♀ 54 mm.

Occurrence.—Males were calling in May from under leaves at the edge of a semi-permanent pond in primary forest. One female lacking ecological data was collected in August.

Life History.—Except for the presence of calling males in May, the only reproductive information available is that a female from August contained 1250 mature ovarian eggs.

Tadpoles.—The tadpoles are unknown.

Mating Call.—The call consists of a long, low-pitched, toad-like trill.

Food.—One individual contained remains of beetles.

Hamptophryne boliviana (Parker)

(FIGURE 113)

Chiasmocleis boliviana Parker, 1927, Occas. Pap. Mus. Zool. Univ. Michigan, 187:3 [Type locality.—Buenavista, Departamento Santa Cruz, Bolivia].

Hamptophryne boliviana.—Carvalho, 1954, Occas. Pap. Mus. Zool. Univ. Michigan, 555:7.

Material.—Dureno, 2; Santa Cecilia, 64+6.

Identification.—This robust microhylid with a pointed snout has a pale dorsum sharply delineated from the darker flanks; the dorsal color on the body is not continuous onto the arms. It differs from the larger *Ctenophryne geayi*, in which the dorsal coloration is continuous onto the arm, by having a dark throat and chest and the rest of the venter pale with dark spots; in *Ctenophryne geayi* the entire venter is dark with pale flecks. The ventral coloration of *H. boliviana* is like that of the smaller *Chiasmocleis bassleri*, which differs by having a dark dorsum not differentiated from the flanks. Other microhylids in the area either have

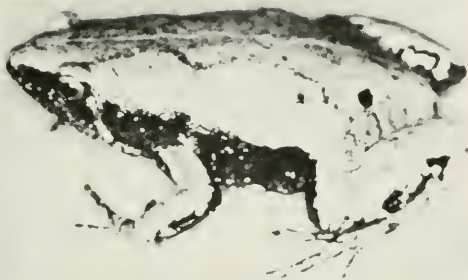


FIG. 113.—*Hamptophryne boliviana*, ♀, 40 mm SVL (KU 124012).

white venters with bold black spots (*Chiasmocleis anatipes* and *C. ventrimaculatus*) or a visible tympanum and only four toes (*Syncope antenori*); *H. boliviana* has a concealed tympanum and five toes.

The body is moderately robust, and the snout tapers medially from the eyes to a narrow truncate tip. The limbs are moderately robust. The fingers and toes have distinct terminal discs and lack lateral fringes and webbing. The skin is smooth above and below. The dorsum is tan or grayish tan with a slightly darker, large, middorsal blotch and usually a narrow, faint, creamy white mid-dorsal line. The flanks, side of the head, and anterior and posterior surfaces of the thighs are dark brown. The dark brown on the flanks separates the pale tan on the dorsum of the body from that on the arm. The throat is dark brown with creamy white flecks. The belly and ventral surfaces of the hind limbs are creamy white with brown to brownish black spots and reticulations. The iris pale bronze with fine black reticulations. Breeding males lack nuptial excrescences. ♂ 38 mm; ♀ 44 mm.

Occurrence.—About 85 percent of the specimens were in mature forest, others were in secondary forest. Most individuals were on the ground at night, but some were in shallow water in ponds and three were perched on leaves of low herbs. One was on the ground by day. Although the frogs were active through-

out the year, 40 percent of the individuals were found in April.

Life History.—Despite the abundance of this species compared to the other microhylids in the area, few data on its life history are available. Males were calling from shallow ponds in April and May. One female from October contained 2186 mature ovarian eggs. Tadpoles were found in April, May, and June, and metamorphosing young were found in June.

Tadpoles.—The following description is based on tadpoles (KU 152564) in stage 27 having a body length of 10 mm and a total length of 30 mm. The body is depressed, about twice as wide as deep, and widest at the level of the orbits. The snout is bluntly rounded. The eyes are small and directed laterally. The spiracle and the cloacal tube are median. The caudal musculature is slender and tapers to a slender tip. The fins are subequal in depth to one another and to the musculature, and the fins extend to the tip of the tail; the dorsal fin does not extend onto the body. The tail is about one-third of the total length. The mouth is terminal and directed ventrally; the fleshy upper lip nearly covers the orifice. Keratinous mouth parts are absent. The dorsum and throat are dark brown; the belly is gray with black mottling. A white stripe is present laterally on the proximal one-third of the caudal musculature.

Tadpoles were found in forest ponds by day when they were swimming individually near the surface.

Mating Call.—The call consists of a moderately long, loud “baaaah.”

Food.—Stomachs of 25 adults were examined. One contained only a small beetle larva. All others contained ants (as many as 47); two also contained Isoptera, and one contained a small beetle and a Dermaptera. *Hamptophryne* was observed feeding on ants at night.

Syncope antenori Walker

Syncope antenori Walker, 1973, Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 20:3 [Type locality.—Puerto Libre, Provincia Napo, Ecuador].

Material.—Puerto Libre, 11.

Identification.—This minute, dull microhylid frog differs from all other frogs in the area by having only four toes and, additionally, from all other microhylid frogs by having a visible tympanum.

This small frog has a robust body and broadly truncate snout in dorsal view. The distinct tympanum is about half of the diameter of the eye. The fingers bear lateral fringes; the four toes (the normal first toe absent) have terminal discs and lack webbing. The dorsum is dull brown; the venter is grayish brown with small bluish white flecks. Males lack nuptial excrescences. ♂ 12 mm; ♀ 14 mm.

Occurrence.—Eight individuals were in primary forest and three in secondary forest in July. All were found at night—four on leaves of low herbs and seven on the ground.

Life History.—Five females contained 5-6 ($\bar{X}=5.4$) ovarian eggs 1.2 mm in diameter. The presence of few relatively large ovarian eggs suggests that in this species eggs may be terrestrial and undergo direct development.

Mating Call.—No call was associated with this species. The absence of vocal slits in adult males perhaps is indicative that this small frog is mute.

Food.—Examination of seven stomachs revealed the presence of ants and mites in six; one of these also contained a small beetle. The seventh individual contained a beetle, a diplopod, and a pseudoscorpion.

TURTLES**CHELIDAE****Chelus fimbriatus** (Schneider)

Testudo fimbriata Schneider, 1783, Allgem. Naturgesch. Schildkr.:349 [Type locality.—Surinam].

Chelys fimbriata—Boulenger, Cat. Chelon. Rhynchoceph. Crocod. Brit. Mus.:209.
Chelus fimbriatus—Mertens, Müller, and Rust, 1934, Bl. Aqua.-Terr. Kunde, 45:65.

Material.—Santa Cecilia, 3.

Identification.—This flattened turtle, commonly called *matamata*, with a broad head and fleshy proboscis is unlike any other Amazonian turtle. The snout and parietal region are orange-tan; the rest of the head and neck are dull dark brown. The limbs are dark brown with a tan stripe along the anterior edge of the forelimb. The carapace is dark brown with a yellowish tan middorsal stripe; the tips of the keels on costal and marginal scutes are tan. The plastron is dull tan. ♂ 330 mm; ♀ 345 mm.

Occurrence.—All of the specimens were obtained from the Río Aguarico by Indians.

Life History.—No data are available.

Mesoclemmys gibba (Schweigger)

Emys gibba Schweigger, 1812, Königsberg. Arch. Naturgesch. Math., 1:299 [Type locality.—unknown].

Mesoclemmys gibba—Gray, 1873, Ann. Mag. Nat. Hist., (4) 11:306.

Material.—Santa Cecilia, 5.

Identification.—This side-necked turtle has a smooth, broad carapace that is flared laterally. It differs from *Phrynops* by having a dark plastron (light in *Phrynops*) and from *Platemys* by having a smooth carapace (two rounded longitudinal ridges in *Platemys*). Furthermore, *Mesoclemmys* has a shallow rounded indentation in the posterior margin of the carapace, whereas *Phrynops* has a deep angular indentation. The carapace and plastron are dark brown to black, and the head and neck are brown. ♀ 214 mm.

Occurrence.—Two were brought in by natives, and two shells were found by a forest pond. Another was in a marsh in a clearing.

Life History.—No data are available.

Remarks.—The two recently killed females were found by a pond in primary

PLATE 1

Dendrobates quinquivittatus



Colostethus sauli



Dendrobates pictus pictus



Colostethus marchesianus



Dendrobates parvulus



Phylllobates femoralis



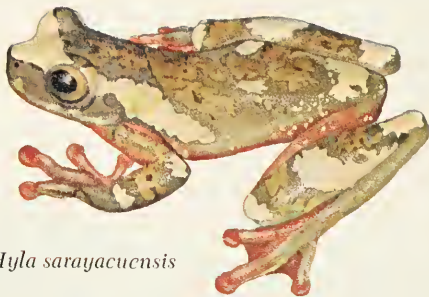
Edalorhina perezii



Lithodytes lineatus



Hyla bifurca



Hyla sarayacuensis



Hyla leucophyllata



Hyla favosa



Hyla triangulum



Hyla triangulum



Hyla minuta



Hyla marmorata



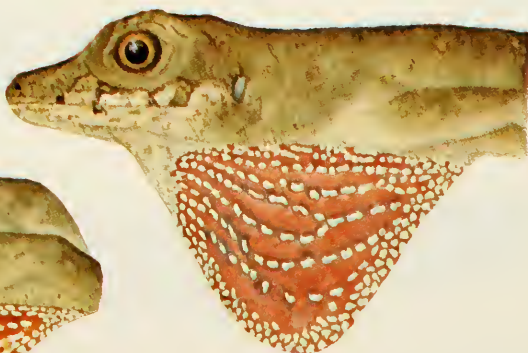
Anolis trachyderma



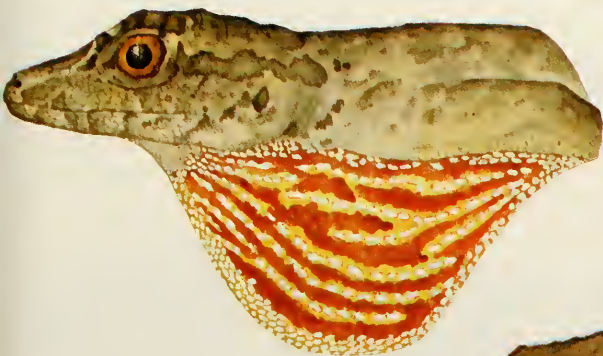
Anolis transversalis



Anolis chrysolepis scypheus



Anolis fuscoauratus



Anolis ortonii



Anolis punctatus boulengeri



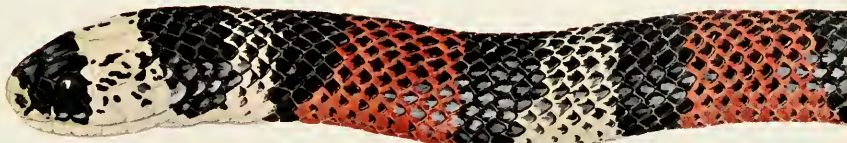
Anilius scytale scytale



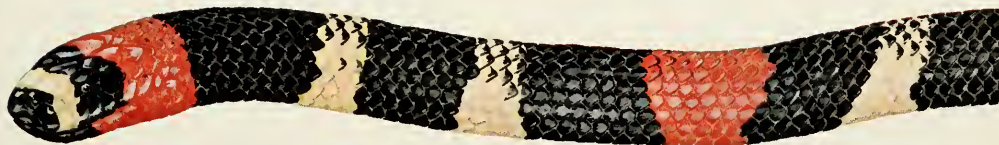
Atractus claps



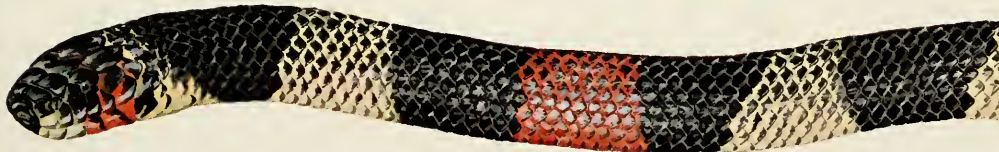
Atractus claps



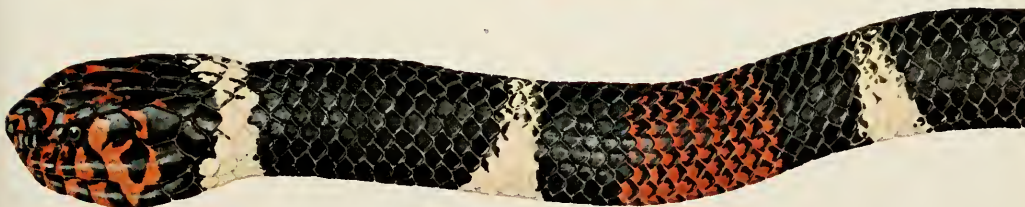
Erythrolamprus aesculapii aesculapii



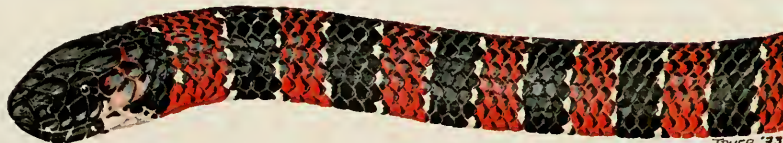
Micrurus lemmiscatus helleri



Micrurus spixii obscurus



Micrurus surinamensis surinamensis



Micrurus langsdorffi langsdorffi

TRUEB '73

forest in April; only shells remained. Conceivably these individuals were seeking oviposition sites when they were attacked by predators. The proximity of the turtles to the large permanent pond suggests that this species may inhabit such ponds and lakes.

***Phrynops geoffroanus tuberosus* (Peters)**

Platemys tuberosa Peters, 1870, Sber. Akad. Wiss. Berlin, 1870:311 [Type locality.—Cotinga River, Mt. Roraima, Guyana].
Phrynops geoffroana tuberosa—Müller, 1939, Physis, 16:95.

Material.—Puerto Ore, 1; Santa Cecilia, 1.

Identification.—*Phrynops geoffroanus* has a broad, smooth carapace that is flared peripherally. The carapace has a deep angular indentation in the posterior margin. The carapace is black. The plastron and ventral flange of the carapace are creamy yellow to orange with black spots. The limbs are dull gray with pale red to creamy white spots. The head and neck are dull olive green with fine black reticulations and a black line from the snout through the orbit and onto the neck. The throat is pale tan with irregular black markings. A pair of long creamy white chin barbels are present. The only other side-necked turtle in the area with a smooth carapace is *Mesoclemmys gibba* which has a black plastron with a shallow rounded indentation in the posterior margin. ♀ 316 mm.

Occurrence.—Both specimens were obtained from the Río Aguarico by natives.

Life History.—No data are available from Santa Cecilia. Medem (1969:334) reported nests containing 10, 11, and 15 eggs found in March and November in Caquetá, Colombia.

***Platemys platycephala* (Schneider)**

Testudo platycephala Schneider, 1792, Schr. Ges. Naturf. Freunde Berlin, 10:261 [Type locality.—“East Indies”].
Platemys platycephala—Boulenger, 1889, Cat. Chelon. Rhynchoceph. Crocod. Brit. Mus.: 227.

Material.—Santa Cecilia, 8.

Identification.—This brightly colored turtle is readily distinguished from other side-necked turtles in the area by its elongate carapace having two rounded longitudinal ridges, bordering a median depression. The shells of *Mesoclemmys* and *Phrynops* lack ridges, and *Chelus* has three keeled ridges. The carapace, plastron, and skin are dark brownish black with an orange-tan periphery to the shell and broad orange stripes on the limbs and dorsum of the head. ♂ 161 mm; ♀ 156 mm.

Occurrence.—A juvenile having a carapace length of 55 mm was in a patch of sunlight in a shallow rivulet in primary forest, and one adult was crawling along a trail by day. One adult was in shallow water in the Río Aguarico by day, and two adults were lying on the bottom of shallow swamps at night.

Life History.—No data are available.

KINOSTERNIDAE

***Kinosternon scorpioides* (Linnaeus)**

Testudo scorpioides Linnaeus, 1766, Systema Naturae, Ed. 12, 1:352 [Type locality.—Surinam].

Kinosternon scorpioides—Gray, 1831, Synops. Rept., 1:34.

Cinosternon scorpioides scorpioides—Siebenrock, 1907, Sber. Akad. Wiss. Wien, 116: 576.

Material.—Santa Cecilia, 9.

Identification.—This small turtle with a high carapace with three low, longitudinal keels withdraws the neck into the shell. Other species with longitudinal ridges or keels on the carapace (*Chelus* and *Platemys*) have low, flattened shells, and fold the neck laterally under the margin of the shell. The other turtle with a high carapace is *Geochelone*, which has short limbs with unwebbed toes; the toes of *Kinosternon* are webbed. The carapace is dull grayish brown; the plastron is dull yellowish brown. The top of the head is yellowish orange with black flecks; the rest of the head, neck, and limbs are dull gray. ♂ 161 mm; ♀ 155 mm.

Occurrence.—One individual was in shallow muddy water in swamp forest, one was in a pond in forest, and one was in a shallow muddy stream in primary forest.

Life History.—No data are available.

Remarks.—Three specimens were found in 1966, five in 1967, and one in 1975. For some inexplicable reason no others were found during the extensive field work in other years.

TESTUDINIDAE

Geochelone denticulata (Linnaeus)

Testudo denticulata Linnaeus, 1766, *Systema Naturae*, Ed. 12, 1:352 [Type locality.—“Virginia”].

Geochelone denticulata—Williams, 1960, *Breviora*, 120:10.

Material.—Lago Agrio, 4; Santa Cecilia, 3.

Identification.—This large tortoise with a domed shell and short, stubby legs is unlike any other turtle in the area. The carapace is dull brown and tan; the plastron is tan. The limbs are brown with orange-tan scales, and the neck is dark brown. The head is yellowish to orange-tan with brown spots in the occipital region. Males have a concave plastron, whereas the plastron in females is nearly flat. ♂ 378 mm; ♀ 328 mm.

Occurrence.—This is a diurnal forest dweller. One was sitting at the base of a stilt palm; two were walking on the forest floor, and one was moving along the edge of the forest in late afternoon.

Life History.—No data are available.

Remarks.—*Geochelone* is eaten by local human inhabitants. On the basis of the number of shells found around Indians' houses, the tortoise must be common in the area. However, with the recent increase in the human population, the number of tortoises can be expected to dwindle rapidly.

CROCODYLIANS

CROCODYLIDAE

Caiman crocodilus crocodilus (Linnaeus)

Lacerta crocodilus Linnaeus, 1758, *Systema Naturae*, Ed. 10, 1:200 [Type locality.—Guyana (restricted by Mertens and Wer-muth, 1955)].

Caiman crocodilus crocodilus—Müller and Hell-mich, 1936, *Wiss. Ergebn. Deutsch. Gran-Chaco Exped.*, Amph. Rept.:110.

Material.—Santa Cecilia, 8.

Identification.—*Caiman* is readily distinguished from the other crocodylian in the area, *Paleosuchus palpebrosus*, by having a bony transverse preorbital ridge and two or three transverse rows of occipital scales. *Paleosuchus* lacks a pre-orbital ridge and has one transverse row of greatly enlarged, strongly keeled occipital scales. *Caiman* has a dull brown or olive-brown dorsum with black transverse marks on the dorsum of the body and sides of the tail. The flanks are yellowish brown, and the lips are olive-tan. The venter is creamy white, and the iris is greenish gray. ♂ 550+350+ mm (in-complete); ♀ 943+1009 mm (extrapolated from skull).

Occurrence.—All individuals were found at night. One juvenile was in the backwater of the Río Aguatico. One adult was in a forest swamp, and two adults and three juveniles were in temporary marshes in clearings. One juvenile came from a lake where many adults were observed at night.

Life History.—No data are available from Santa Cecilia. Medem (1969:330) reported on a nest of this species on the Río Caquetá (Amazon drainage) in Colombia. The nest, containing 24 eggs, was found in 16 March. Hatchlings had snout-vent lengths of 115.5–123.0 mm. These are noticeably smaller than the smallest juveniles from Santa Cecilia (230, 275, 285 mm). Of these, the one having a snout-vent length of 230 mm was found on 16 March. The other two are from April. In light of Medem's data it is probable that *Caiman* has an extensive reproductive season.

Remarks.—Hunting pressure and wanton killing of *Caiman* by the increasing human population seems to have decreased the population of *Caiman* in the

lakes at Santa Cecilia. In 1967 scores of *Caiman* (as determined by their red eyeshine) were observed on various nights. In 1971 and 1972 only a few could be seen on any given night.

***Paleosuchus trigonatus* (Schneider)**

Crocodilus trigonatus Schneider, 1801, Hist. Amph., 2:161 [Type locality.—unknown].
Paleosuchus trigonatus—Schmidt, Field Mus. Nat. Hist. Zool., 12:209.

Material.—Lago Agrio, 3; Santa Cecilia, 5.

Identification.—*Paleosuchus* is readily distinguished from the only other crocodilian in the area, *Caiman crocodilus*, by lacking a bony transverse preorbital ridge and by having a single transverse row of greatly enlarged, strongly keeled occipital scales. *Caiman* has a preorbital ridge and two or three transverse rows of small occipital scales. *Paleosuchus* is dull brown dorsally with broad, dark brown and orange-tan bars on the tail. The venter and lower jaw are cream with large, brownish-gray spots. The iris is brown. ♂ 465+410 mm; ♀ 837+732 mm (extrapolated from skull).

Occurrence.—All were found at night. One juvenile was in a muddy depression in second growth forest near the river; two were in small streams, and one was in the Río Aguarico. Ecological data are lacking for the other specimens.

Life History.—No data are available.

Remarks.—Seemingly the two crocodilians in the area have different habitat preferences. *Caiman* inhabits lakes and swamps, whereas *Paleosuchus* primarily inhabits streams and rivers with a strong current. These observations corroborate those of Medem (1952) on *Paleosuchus trigonatus* in Colombia. The large black caiman, *Melanosuchus niger*, apparently does not occur in the upper Río Aguarico. According to Medem (1963), it inhabits slowly flowing rivers. Medem reported it from the Río Putumayo in Colombia, and there are specimens at The University of Kansas from the Río Napo in Ecuador.

LIZARDS

Gekkoniidae

***Gonatodes concinnatus* (O'Shaughnessy)**

(FIGURE 114)

Material.—Lago Agrio, 5; Santa Cecilia, 27.

Identification.—This small gecko has claws that are not covered by a scaly sheath, and the scales on the belly are broadly rounded posteriorly. In these respects it differs from the other small gecko in the area, *Pseudogonatodes guianensis* in which the claws are retractile into a scaly sheath, and the scales on the belly are pointed posteriorly. Female *Gonatodes* can be confused with small *Anolis*. In the latter, scaly, moveable eyelids are present, the digits are dilated, and the scales on the top of the head are not granular. Furthermore, *Anolis* have much longer limbs and tails.

The scales on the dorsal and lateral surfaces of the body are small and granular; the ventral scales are noticeably larger, ovoid, and flat. Striking sexual dimorphism exists in coloration. In both sexes a white collar is evident and usually interrupted dorsally; the collar is narrow in females and much wider, especially ventrolaterally, in males. The head and neck are orange or reddish brown with cream spots in males; the body is olive green with reddish brown reticulations, and the tail is black with white rings. The throat is orange with cream streaks, and the belly is yellowish gray. In females the head, body, and tail are grayish tan with irregular brown markings, some of which are crescent-shaped in a pair of dorsolateral rows; the spots on the tail tend to be fused across, giving the tail a banded appearance. The venter is creamy tan. The iris is reddish brown with a cream circle around the pupil. Juveniles are colored like females. Individuals having regenerated tails lack bands or rings on the tail. ♂ 52+45 mm (incomplete); ♀ 49+46 mm.

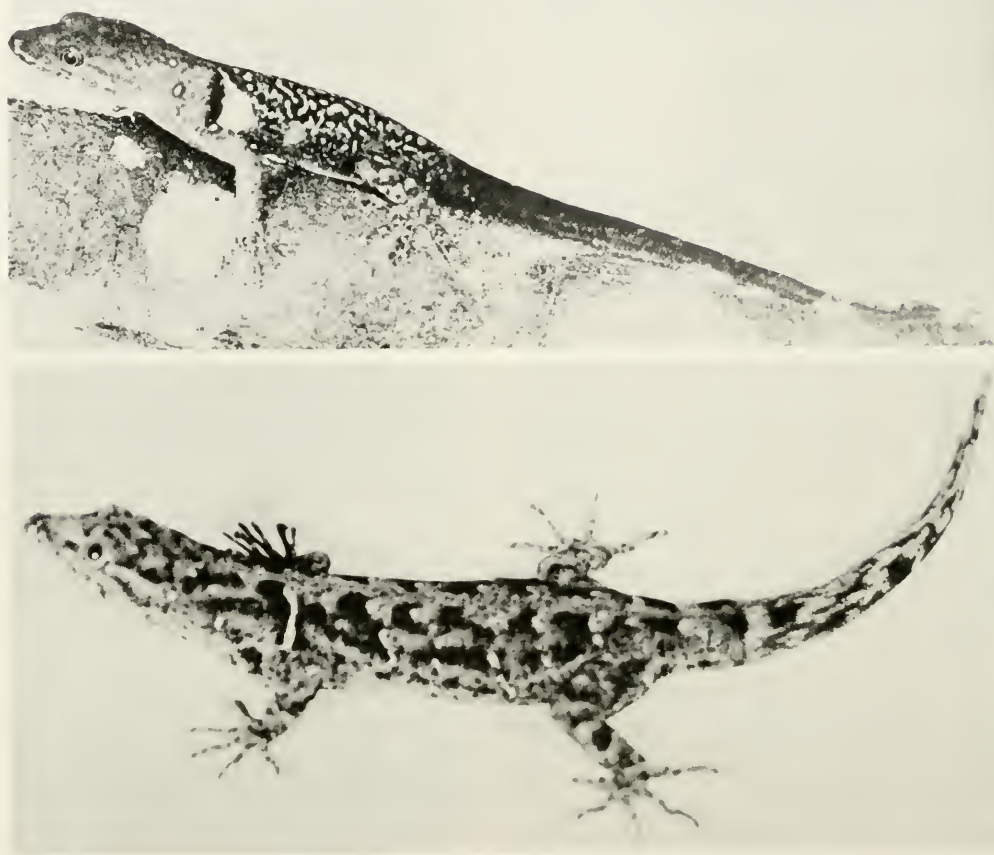


FIG. 114.—*Gontodes concinnatus*, Upper: ♂, 41 mm SVL (KU 146643). Lower: ♀, 48 mm SVL (KU 146645).

Occurrence.—By day, most individuals were found on trunks of large trees in primary forest; one was found in leaf litter on the forest floor. All were in shade. At night, individuals were sleeping horizontally on leaves or stems of bushes and vines; usually adjacent to tree trunks. One was on a log in a clearing at night.

Life History.—Six females (March 1, April 3, May 1, August 1) each contained one egg; the smallest of these females had a snout-vent length of 34 mm. The largest oviducal egg was 10.4 mm in length. The two smallest juveniles (snout-vent lengths of 17 and 19 mm) were obtained in July. These limited data, together with those summarized by

Fitch (1970:20), suggest that *Gonatodes* probably reproduces throughout the year with the possible exception of the drier months (December-February).

Food.—A variety of small arthropods was eaten. In both frequency and volume, five items are about equal (spiders, beetle larvae, termites, roaches, and hemipterans). These comprise 61.3 percent of the frequency and 56 percent of the volume in 10 stomachs.

***Pseudogonatodes guianensis* Parker**
(FIGURE 115)

Material.—Puerto Libre, 6; Santa Cecilia, 11.

Identification.—This minute lizard,



FIG. 115.—*Pseudogonatodes guianensis*, ♀, 26 mm SVL (KU 146646).

the smallest species in the area, has claws that are retractile into a scaly sheath; it differs in this respect from the slightly larger gecko, *Gonatodes concinnatus*, in which the claws are not covered by a scaly sheath. Furthermore, in *Pseudogonatodes* the posterior margins of the belly scales are pointed, whereas they are broadly rounded in *Gonatodes*. Both *Gonatodes* and *Pseudogonatodes* lack movable lower eyelids, a characteristic shared with a third gecko, *Thecadactylus rapicauda*, which has greatly dilated toes and large tubercles interspersed among the granular dorsal scales. *Gonatodes* and *Pseudogonatodes* have uniform granular scales on the dorsum and cylindrical or laterally compressed toes.

The dorsum is dull brown. Usually the pattern consists of an orange-tan transverse band on the neck and posterior part of the head and small orange-tan spots in two dorsolateral rows. In some individuals a yellowish-tan dorsolateral stripe is evident on the proximal half of the tail. Some individuals are darker brown or gray and have an obscured pattern. Usually two cream bars are present on the lip. The chin and throat are white with brown or gray longitudinal streaks, and the belly is tan or gray. The iris is orange-tan. ♂ 26+21 mm; ♀ 27+23 mm.

Occurrence.—This small lizard is active amidst shaded leaf litter on the forest floor by day. Nine of 13 individuals

were in primary forest; two were in secondary forest, and two were at the edge of the forest.

Life History.—One female from April contained one egg 5 mm in length, and one from July contained one egg 6 mm in length. All other females were obtained in May, June, and July; five contained small ovarian eggs, and one showed no evidence of reproductive activity.

Food.—In 11 stomachs five food items comprised 93.3 percent of frequency and 90.9 percent of volume — spiders, sow bugs, beetle larvae, termites, and small orthopterans.

Taxonomic Comments.—The morphological characters of the Ecuadorian specimens support Hoogmoed's (1973: 96) contention that *Pseudogonatodes amazonicus* Vanzolini is indistinguishable from *P. guianensis*.

***Thecadactylus rapicauda* (Houttuyn)**

(FIGURE 116)

Material.—Lago Agrio, 4; Santa Cecilia, 9.

Identification.—This large, robust gecko has two rows of greatly expanded pads on the underside of each toe; the dorsum of the body is covered with minute granular scales with larger tubercles interspersed. These characters serve to distinguish *Thecadactylus* from all other lizards in the area.

The dorsum is tan, orange-tan, or

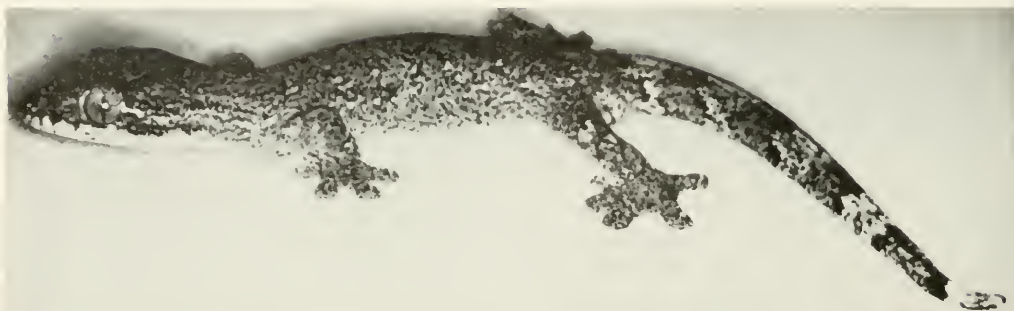


FIG. 116.—*Thecadactylus rapicauda*, ♂, 53 mm SVL; Barro Colorado Island, Canal Zone (KU 75768).

grayish tan with irregular dark brown or black lines on the head and neck and narrow dark markings on the body. The latter markings vary from short dashes to rhomboidal marks enclosing pale areas of the ground color. A quadrangular or diamond-shaped black or brown spot usually is present at the base of the tail, and two or three such markings are present on original tails. The flanks are dark brown or colored like the dorsum; if the latter, a dark brown ventrolateral stripe extends from the eye to the base of the hind limb. The venter is pale yellowish tan; the iris is reddish tan. ♂ 108+91 mm; ♀ 112+84 mm.

Occurrence.—This is the only nocturnal lizard in the area. One individual was found in a thatched roof at dusk, one was on a box next to a building at night, and others were observed on banana plants at night. Four were obtained from trees when primary forest was being cleared.

Life History.—Four females each contained one oviducal egg 18-22 ($\bar{X}$ =19.0) mm in length; the females were obtained in May (2), June, and August.

Food.—In seven stomachs, roaches comprised 70 percent of the volume. One individual contained a scorpion.

IGUANIDAE

Anolis chrysolepis scypheus Cope

(PLATE 3)

Anolis scypheus Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia 1864:172 [Type locality.—not given].

Anolis chrysolepis scypheus—Vanzolini and Williams, 1970, Arq. Zool., São Paulo 19:85.

Material.—Dureno, 2; Lago Agrio, 6; Puerto Ore, 1; Santa Cecilia, 167.

Identification.—This moderately large anole has a robust body and proportionately, a large head with a short snout. The dorsum is predominately brown, and the dewlap is red peripherally and blue medially with white scales. No other anole in the area has a similarly colored dewlap. Females can be distinguished from other anoles by the large head, small keeled supraorbital scales, large keeled ventral scales, and the presence of a small dewlap. *Anolis ortonii* is the species most easily confused with *Anolis chrysolepis*; the former has larger smooth supraorbital scales and smooth ventral scales. Furthermore, the dewlap in *Anolis ortonii* is orange with red streaks.

The dorsum is variegated brown, reddish brown, tan, and/or gray. Usually in males and occasionally in females, there is a narrow, yellowish tan, longitudinal middorsal stripe on the posterior part of the body and base of the tail. The dorsal pattern in males usually consists of dark brown or reddish brown diagonal marks or semicircles (closed edge dorsally). The top of the head is brown with a dark brown interorbital bar. Most females have a broad middor-

sal gray or tan stripe bordered by a broad brown area. The venter is pinkish cream in females and rusty red or burnt orange in adult males. The dewlap is blue medially with white scales and a broad red periphery. The iris is tan. ♂ 84+182 mm; ♀ 86+170 mm.

Occurrence.—This primarily terrestrial anole inhabits both primary and secondary forest. Although a few individuals have been observed basking on logs or buttresses, most have been seen actively foraging in the shade. The majority of the lizards were found sleeping at night. Usually the lizards were horizontal on a branch of a bush less than 1.5 m above the ground, and some were found head up on sticks or stems close to the ground. Only two were found on branches more than 1.5 m above the ground.

Although *Anolis chrysolepis* climbs on logs or buttresses of trees during its normal diurnal activity, it is primarily a terrestrial species. Individuals run short distances on the ground and then remain motionless; their coloration blends well with the leaf litter on the forest floor. Fitch (1968:36) reported body temperatures of eight specimens as 24.0–32.8°C ($\bar{X}=27.5\pm0.88$) with a mean deviation from air temperature of $+1.51\pm0.77^\circ\text{C}$; he discussed these lizards under the name *Anolis scypheus*.

Life History.—Gravid females have been found from March through November; only three specimens of the species were obtained from December through February. Six females each contained one oviducal egg, and seven contained two eggs, length 15.4–19.6 ($\bar{X}=17.1$, $N=20$) mm.

One individual having a snout-vent length of 29 mm hatched on 31 October from an egg found on 22 September. Juveniles having snout-vent lengths of 28–31 mm were found from March through October. These data and those on gravid females strongly suggest that reproduction occurs throughout the year.

Food.—In 25 specimens examined,

orthopterans comprised 28 percent of the volume of food, and beetle larvae, 11.2 percent. The other seven categories of food were found in small amounts. One was observed eating a microteiid lizard, *Leposoma parietale*, and one contained the tail of an *Anolis trachyderma*.

Anolis fuscoauratus fuscoauratus

D'Orbigny

(PLATE 3)

Material.—Lago Agrio, 27; Puerto Libre, 15; Puerto Ore, 3; Santa Cecilia, 163.

Identification.—This small anole is identifiable chiefly by the absence of any one distinguishing character. All of the head scales are small and keeled; the ventrals are small, smooth, and nearly granular. The dorsum is gray or dull tan; many females have a pale tan middorsal stripe. The chin, throat, and belly are grayish white with brown or dark gray flecks. In males the large dewlap is rose-pink with white scales and a white margin. The iris is brown. *Anolis fuscoauratus* is most easily confused with *A. trachyderma* and *A. ortonii*. The former has larger, flat, smooth scales ventrally and a transverse yellow line on the chin; the small dewlap is orange-red with black scales. *Anolis ortonii* has flat, smooth ventral scales and smooth head scales. The dorsum of *A. ortonii* is tan or pale gray with brown mottling; the large dewlap is orange with red streaks. Juveniles of *A. punctatus* can be distinguished from *A. fuscoauratus* by the former having keeled ventral scales and keeled scales on the tip of the snout, whereas the other head scales are smooth. ♂ 43+85 mm; ♀ 47+92 mm.

Occurrence.—Although this small lizard frequently is seen on the forest floor by day, individuals are most easily collected at night when they are sleeping horizontally or head-down on grasses, herbs, or limbs of bushes, usually at heights of less than 1 m from the ground. During the day, *Anolis fuscoauratus* for-

ages in shade on the forest floor; only four were observed sunning – three on logs and one on a low bush. The local distribution of the species is most accurately determined by the occurrence of sleeping individuals, most of which are associated with forest – primary forest 26 percent, secondary forest 52 percent, and forest edge 15 percent. Three individuals were found in clearings, and nine in banana groves.

Individuals were found throughout the year, but only four were taken in the drier months (December-February).

Life History.—The smallest females with mature ovarian eggs have snout-vent lengths of 37 mm or more and have been found in every month except January and February. No females were found in January, and the only one taken in February had immature ovarian eggs. More than 40 percent of the females taken in each of five months (March-July) contained oviducal eggs. Of 52 females containing oviducal eggs, 33 had one egg, and 18 had two eggs. Of 36 females containing large ovarian eggs, 30 had one egg, and six had two eggs.

Four females each laid a single egg in captivity. Eggs were deposited on 2 March, 4 October, and 14 and 21 December. They required 53-63 ($\bar{x}=57$) days to hatch. The eggs varied in size from 9×5 mm to 9.5×6 mm. The hatchlings had snout-vent lengths of 16-19 ($\bar{x}=17.4$) mm.

Apparently, *Anolis fuscoauratus* usually deposits single eggs throughout the year. The presence of two equally well-developed eggs in the reproductive tract at a given time indicates that clutches of two may be deposited or that the eggs are laid separately at short intervals.

Food.—In 25 stomachs, small spiders and orthopterans comprised half of the volume of food. Ants made up 11 percent of the volume, whereas other kinds of food were present in small quantities.

Remarks.—The ecological relationships of *Anolis fuscoauratus* and *A. trachyderma* are discussed in the account of the latter species.

Anolis ortonii Cope

(PLATE 3)

Material.—Lago Agrio, 3; Santa Cecilia, 9.

Identification.—This small tan or pale gray anole has large smooth ventral scales; the supraorbitals are large and smooth. The scales on the tip of the snout are keeled, but the other head scales are smooth. Both *Anolis fuscoauratus* and *A. trachyderma* have keeled dorsal head scales and small keeled supraoculars; the ventral scales in these species are smaller than those in *A. ortonii*. The large dewlap in *A. ortonii* is orange with red streaks, whereas the dewlap in *A. fuscoauratus* is large and rose-pink with white scales, and that in *A. trachyderma* is orange-red with black scales. The dorsal coloration of *A. ortonii* is tan or pale gray with brown streaks on the body and a dark brown interorbital bar. The throat is brown with dark brown diagonal bars evident in most adult males. The venter is creamy tan, and the iris is brown. ♂ 50+64 mm; ♀ 43+68 mm.

Occurrence.—Half of the 12 specimens were obtained in June and July; others were found in March (1), April (2), May (2), and November (1). Two individuals were found on a thatched roof in a clearing. All others were in forest (five in primary, two in secondary). One was on a tree trunk, one on the branch of a low bush, and three were on the ground. Two were sleeping on low bushes at night. These limited observations suggest that *A. ortonii* is primarily terrestrial but does ascend tree trunks and low bushes during its period of activity.

Life History.—Two females (one from May and one from July) each contained two oviducal eggs 10.5 and 10.3 mm in length. Two females from June and July contained large ovarian eggs. No juveniles were found.

Food.—Ants formed the most numerous food item in seven stomachs and comprised 53.6 percent of the volume. Other food items included spiders and

orthopterans, including one mole cricket (Gryllotalpidae).

Anolis punctatus boulengeri

O'Shaughnessy

(PLATE 3)

Material.—Lago Agrio, 7; Santa Cecilia, 10.

Identification.—The green dorsum and yellow scales around the eye immediately distinguish this large anole from its sympatric congeners. The snout is long, and the scales on the tip of the snout are keeled; the other head scales are smooth, and the supraorbitals are enlarged. The ventral scales are weakly keeled. The dewlap is large and yellow or orange-yellow with pale yellow or white scales. The only other large anole in the area is *Anolis transversalis*, which has smooth head scales and ventrals and a large orange or pale yellow dewlap with black or dark brown streaks or bars; furthermore, the dorsum of *A. transversalis* has diagonal black or dark brown marks.

The dorsum of *Anolis punctatus* is bright green with pale cream or bluish white flecks laterally and dorsolaterally and tan middorsally. The throat and scales around the eye are yellow; the tail is tan distally. The belly and ventral surfaces of the limbs are creamy white to pale tan with brown flecks. The iris is bronze. ♂ 82+170 mm; ♀ 77+202 mm.

Occurrence.—Individuals were found in all months, except November through January; seven were obtained in May from trees as they were felled at Lago Agrio. Three individuals were sleeping on bushes at heights of less than 1.5 m above the ground, and one juvenile was sunning on a log. All were found in forest.

Life History.—All 11 females contained eggs; two females taken in May each had one oviducal egg (17.1 and 18.1 mm in length), and one found in August had two oviducal eggs 16.2 mm in length. Females having mature ovarian eggs were found in July and October, and

females from February through July contained immature ovarian eggs. Thus, the limited evidence suggests reproductive activity throughout the year. The only juvenile has a snout-vent length of 49 mm and was obtained in September.

Food.—In 14 stomachs, three groups of insects comprised 76.8 percent of the volume of food: orthopterans (30.4%), ants (28.6%), and beetles (17.8%).

Anolis trachyderma Cope

(PLATE 3)

Material.—Lago Agrio, 3; Puerto Libre, 9; Santa Cecilia, 308.

Identification.—This small, drab lizard is darker colored by day than any other anole in the area. It can be distinguished from the other species by its dark chin with one or two narrow, transverse cream or yellow lines. The dorsal head scales are keeled, and the ventral scales are small, flat, and smooth. In males, the base of the tail is greatly swollen, and the dewlap is small and orange-red with black scales. *Anolis fuscoauratus* and *A. ortonii* are about the same size, but both lack transverse light lines on the chin; the base of the tail is not swollen in males, and the dewlap is differently colored—rose pink with white scales in *A. fuscoauratus* and orange with red streaks in *A. ortonii*.

At night *Anolis trachyderma* is pale tan with little or no evidence of pattern. By day, it is brown with dark brown markings: interorbital bar, two diagonal bars on lips, stripe extending posteriorly from eye, and in some males small chevrons middorsally on body and base of tail. Narrow, cream diagonal lines are present on the forearm and shank. In many females a reddish brown middorsal stripe is bordered by a narrow, irregular tan line; in some females small yellowish tan vertical bars are evident dorsolaterally on either side of the middorsal stripe. The brown dorsal color extends onto the ventrolateral surfaces of the body. The belly is cream or yellow, usually flecked with brown. The iris is reddish brown. ♂ 51+106 mm; ♀ 58+89 mm.

Occurrence.—This small anole is active on the forest floor and in low vegetation. Approximately twice as many individuals were observed on the ground and in leaf litter as were seen in bushes. None was observed in direct sunlight, nor was the species found in clearings or cultivated areas. Of 265 individuals found sleeping, usually head up or horizontally on low vegetation at night, 52 were in primary forest, 195 were in secondary forest, and 18 were in forest-edge situations.

Life History.—Reproduction apparently takes place throughout the year. No females were obtained in January; two were collected in December, and both contained immature ovarian eggs. Females containing oviducal eggs were found in all of the other months. No females having snout-vent lengths of less than 45 mm contained large ovarian or oviducal eggs, although females having snout-vent lengths of 40-45 mm contained small ovarian eggs. Each of eight females contained two oviducal eggs, and 36 had one egg each. Lengths of oviducal eggs were 12.4-15.4 ($\bar{x}$ =13.6, N =52) mm.

Three captive females laid single eggs on 7 February, 15 September, and 22 November; the latter hatched 77 days later on 7 February. One egg found in leaf litter on 19 July hatched on 10 August, and one found in leaf litter on 22 September hatched on 6 November. The eggs varied in size from 10 × 3.4 mm to 14 × 6 mm. The hatchlings had snout-vent lengths of 22.0-23.0 mm. Sixteen recent hatchlings having snout-vent lengths of 23-29 mm were found in March (2), May (1), June (5), July (4), August (1), September (1), and October (2). The dates for hatchlings seem to reinforce the data on oviducal eggs in providing evidence for acyclic reproduction in this species, but no recent hatchlings were found in the drier months (December-February).

Food.—In 27 stomachs, spiders comprised 42.2 percent of the volume; nine

TABLE 6.—Comparative Data on Abundance of *Anolis fuscoauratus* and *Anolis trachyderma* at Santa Cecilia.

HABITAT	<i>A. fus-</i> <i>coauratus</i> (<i>N</i> =164)	<i>A. trachy-</i> <i>derma</i> (<i>N</i> =283)
	Percentage Occurrence	
Primary Forest	26%	20%
Secondary Forest	52%	73%
Forest Edge	15%	7%
Clearing	7%	0%
DATE	Frequency of Occurrence	
March 1967	17	14
June 1967	19	7
June 1968	22	35
August 1971	2	35
October 1971	8	19

other kinds of arthropods were present in much smaller amounts.

Remarks.—In comparison with *Anolis fuscoauratus*, *A. trachyderma* seems to be more restricted in its ecological distribution and a less frequent inhabitant of primary forest. This conclusion is borne out by three sets of data. The majority (73%) of *A. trachyderma* was taken in secondary forest, whereas only 52 percent of the *A. fuscoauratus* was found there. *Anolis fuscoauratus* was found in clearings, but no *A. trachyderma* was found there (Table 6). At Lago Agrio when primary forest was being cleared in May 1969, all anoles seen were captured — 27 *A. fuscoauratus* and three *A. trachyderma*. In early collections from Santa Cecilia, when most of the forest was undisturbed (1967-68), the two species were found in nearly the same frequency, whereas in later collections (1971), when much of the primary forest had been partially lumbered, *A. trachyderma* was found in far greater abundance than *A. fuscoauratus* (Table 6). Thus, it seems evident that although *A. fuscoauratus* has broader ecological tolerances than *A. trachyderma*, the latter species is increasing in relative abundance with the increase in the amount of secondary forest.

Anolis transversalis Duméril
(PLATE 3)



FIG. 117.—*Enyalioides cofanorum*, ♀, 107 mm SVL (KU 146658).

Material.—Lago Agrio, 3.

Identification.—This large anole is readily distinguished from all other anoles in the area by having smooth head scales and a distinctive color pattern of transverse markings on the body. The dorsal coloration changes from dark brown to black. The dark transverse markings are diagonal posteroventrally onto the edge of the belly and vary from four broad to six or seven narrow marks on the body and about an equal number on the tail. A dark vertical bar extends ventrally from the eye, and another from the ear. The throat and belly are cream, and the dewlap is yellow with bold black or dark brown vertical bars or narrow gray or bluish gray diagonal lines. Dewlaps are present in both sexes. The iris is bright blue. ♂ 72+104 mm; ♀ 72+100 mm.

Occurrence.—Three specimens were obtained from high branches of large trees as they were felled. Presumably the species lives only in the foliage of the upper story of primary forest.

Life History.—The single female ob-

tained in May contained one ovarian egg 14.4 mm in length.

Food.—All three specimens contained only beetles.

Enyalioides cofanorum Duellman

(FIGURE 117)

Enyalioides cofanorum Duellman, 1973, *Herpetologica* 29:230 [Type locality.—Santa Cecilia, Provincia Napo, Ecuador].

Material.—Santa Cecilia, 11.

Identification.—*Enyalioides cofanorum* is a moderately large lizard with a large, chunky head, a middorsal crest of enlarged spiny scales, and keeled spinous caudal scales arranged in whorls. The species resembles *Enyalioides laticeps festae* but differs in that the latter has homogeneous scales on the dorsolateral surfaces of the body; *E. cofanorum* has a dorsolateral row of distinctly enlarged, conical scales on the body. *Plica umbra ochrocollaris* superficially resembles both species of *Enyalioides*, but it is a smaller, more slender lizard with larger scales on the body, smaller caudal scales not an-



FIG. 118.—*Enyalioides laticeps festae*, ♂, 114 mm SVL (KU 122106).

ranged in whorls, and a blue lining of the mouth (pink in *Enyalioides*).

Adults are dark brown with scattered greenish yellow scales on the back and lips. The throat is brown with scattered cream scales, and the belly is tan. Juveniles are dark brown with yellowish tan cross bars and black spots along the dorsal crest. There is a yellow diagonal bar from the ear to the shoulder; the head is rusty brown. The chin is grayish white, and the belly is cream. The iris is orange-brown. ♂ 101+118 mm; ♀ 107+120 mm.

Occurrence.—Five of nine individuals were found in primary forest; the others were in secondary forest. Two were active by day on the forest floor (one was on a log). By night individuals were found sleeping head-up on sticks or horizontally on limbs of bushes, all less than 1.5 m above the ground.

Life History.—Of six adult females, two were found in July and one each in

March, June, August, and September. One female taken in March contained two ovarian eggs 26.3 mm in length; one taken in July had two oviducal eggs 28.4 mm in length. The smallest juveniles, having snout-vent lengths of 55 and 57 mm, were taken in April and June, respectively.

Food.—Six individuals contained five kinds of food in nearly the same volumes: earthworms, sow bugs, spiders, beetles, and orthopterans.

Remarks.—Comparative ecological data on the two species of *Enyalioides* are given in the following account.

Enyalioides laticeps festae Peracca

(FIGURE 118)

Material.—Dureno, 1; Lago Agrio, 11; Puerto Libre, 1; Santa Cecilia, 46.

Identification.—This moderately large lizard has a chunky head and a middorsal crest of large spiny scales; the keeled,

spinous scales of the tail are arranged in whorls. *Enyalioides laticeps festae* is most easily confused with two other iguanids of about the same size – *Enyalioides cofanorum* and *Plica umbra ochrocollaris*. The latter has a proportionately smaller head and weakly keeled caudal scales not arranged in whorls; furthermore, the lining of the mouth is blue in *Plica* and pink in *Enyalioides*. The two species of *Enyalioides* are easily distinguished by the nature of the scales on the body. In *Enyalioides laticeps festae* the dorsal scales, except the middorsal row, are of uniform size; in *E. cofanorum* there is a dorsolateral row of distinctly enlarged, conical scales. Some preserved specimens of *E. laticeps festae* appear to have a dorsolateral row of enlarged scales, but in reality, this appearance is due to a fold of skin, an artifact of preservation.

In adults the dorsum varies from dull green to brown with paler, irregular spots dorsolaterally, faintly expanded into diagonal bars in some specimens. Usually the top of the head is dull olive green, and the rest of the dorsum is dull olive green with tan or pale orange spots or diagonal bars. The lips are green, and blue or blue-green scales are present ventrolaterally on the body and on the limbs. The chin is pale green. In males the throat is streaked orange, brown, and green; the gular region is dark brown, and the belly is orange. In females the gular region is rusty red, and the belly is pinkish tan. In many specimens there is a pale orange or tan diagonal blotch on the side of the neck. Most adult males have an orange stripe from the corner of the mouth to a point below the ear. The iris is brown with a yellow or greenish yellow ring around the pupil. Juveniles are pale green or tan with brown or reddish brown diagonal markings on the body; the throat is white (with red streaks in some), and the belly is creamy tan. ♂ 128+200 mm; ♀ 125+202 mm.

Occurrence.—*Enyalioides laticeps festae* is a diurnal inhabitant of primary

forest; 80 percent of the individuals were found in primary forest, whereas the others were in secondary forest. One was observed on the ground by day; 17 others were on vegetation. By day, the species usually is observed on trunks of small trees or palms having a diameter of less than 15 cm; one was found on a bamboo. Especially in the mornings, the lizards sun head-up on the trunks; when disturbed they move around and up the trunk. At night the lizards sleep, usually nearly horizontally, on branches or palm fronds, usually at heights of more than 1.5 m above the ground. Some sleep head-up on trunks of saplings.

Life History.—No females were found in October through February; females with immature ovarian eggs were found in March through September. One female with mature ovarian eggs was found in March, and four were found in May. These five females have snout-vent lengths of 107-125 ($\bar{x}=114$) mm. The number of eggs in each varied from 5 to 7 ($\bar{x}=6.2$), and lengths of the eggs were 15.0-16.6 ($\bar{x}=15.6$) mm. Adult males were found in March through November. The three smallest juveniles have snout-vent lengths of 43, 45, and 57 mm and were found in March, April, and March, respectively.

The reproductive data are inconclusive with regard to seasonality. The absence of reproductively active females from October through February probably is due to inadequate sampling, because the smallest juveniles were taken in March and April. Presumably, the species breeds throughout most or all of the year.

Food.—In 24 stomachs, three food items comprised 70.4 percent of the volume: spiders (37.5%), caterpillars (20.4%), and beetle grubs (12.5%). The other 29.6 percent was made up of eight different groups of invertebrates, of which orthopterans comprised 8.2 percent.

Remarks.—*Enyalioides cofanorum* and *E. laticeps festae* principally inhabit pri-



FIG. 119.—*Plica umbra ochrocollaris*, ♂, 89 mm SVL (KU 146659).

mary forest; the former species apparently is terrestrial, whereas the latter seems to be primarily arboreal. Thus, the two species seem to be ecologically segregated.

Plica umbra ochrocollaris (Spix)

(FIGURE 119)

Material.—Lago Agrio, 5; Santa Cecilia, 27.

Identification.—This lizard is immediately distinguishable from all others in the area by having a middorsal crest and large, pointed, keeled scales of uniform size on the body and tail; the scales on the tail are not arranged in transverse whorls. *Plica* is most easily confused with *Enyalioides*, the only other lizards in the area having middorsal crests, but *Enyalioides* has small granular scales on the body, caudal scales arranged in transverse whorls, a large chunky head, and the lining of the mouth pink. *Plica* has a proportionately smaller head and the lining of the mouth blue.

The dorsal coloration is highly variable. Some males are bright green with small black spots in a dorsolateral row; others are dull olive-green or olive-tan, as are females. The tail is olive-tan above

and reddish tan below. In all individuals a black mark is present below the eye and another is present at the angle of the jaw. A narrow black line extends posteriorly from the eye and connects (or nearly so) with a narrow black collar that is incomplete middorsally. The area below the line is creamy white to reddish brown. The throat is grayish brown, reddish brown, or greenish gray, and the belly is pale grayish brown to reddish brown. The iris is orange or reddish tan. ♂ 89+204 mm; ♀ 90+181 mm.

Occurrence.—All individuals were associated with forest (12 in primary, 18 in secondary). One was sunning on a log at the edge of the forest, and five were obtained as trees were felled in primary forest. Twenty individuals were sleeping at night horizontally on branches, palm fronds, or bamboo twigs; one was head-up on a tree trunk. Most sleeping individuals were at heights of less than 1.5 m above the ground, but five were at greater heights, one at 4 m. Nine of 20 sleeping individuals were on perches over swamps or streams.

Life History.—Three females (March 2, August 1) each contained two oviducal eggs 23.0-26.7 ($\bar{x}$ =24.6) mm in



FIG. 120.—*Polychrus marmoratus*, ♀, 148 mm SVL (KU 142870).

length. One from May contained four maturing ovarian eggs 16.5 mm in length. All other females were taken in April through November and all contained small ovarian eggs. The smallest of these lizards has a snout-vent length of 69 mm. The smallest juvenile has a snout-vent length of 45 mm and was obtained in August. Beebe (1944:208) noted that in Guyana *Plica umbra* was in breeding condition in April, May, and October.

Food.—Eleven individuals contained only ants in their stomachs. Beebe (1944:208) reported beetles, orthopterans, and centipedes, in addition to ants, in lizards from Guyana.

Polychrus marmoratus (Linnaeus)

(FIGURE 120)

Material.—Dureno, 2; Santa Cecilia, 7.

Identification.—This large, green (brown in preservative) lizard with white and yellow markings and a long tail is easily recognized. The toes are not dilated, and the third and fourth toes are equal in length. The body and

tail are covered with smooth, overlapping scales of uniform size; a middorsal crest is absent. The dorsum is green with reddish brown crossbars. The narrow postorbital and suborbital stripes are black. The pale green venter is separated from the darker green dorsum by irregular ventrolateral white markings on the body, tail, and anterior edge of the hind limb. The iris is reddish brown; the tongue is fleshy pink; and the lining of the throat is black. ♂ 122+330 mm; ♀ 148+321 mm.

Occurrence.—This arboreal species is a forest inhabitant. Precise ecological data are lacking for most of our specimens. In October 1971 one adult female, one adult male, and two juveniles were obtained at the edge of the forest. These were sleeping at heights of 1-2 m; one was head-down on a clump of cane-like grass, and the others were on horizontal limbs of bushes. The male and one juvenile were in a swamp.

Life History.—Two adult females (July and October) are available; both contain small ovarian eggs. The smallest



FIG. 121.—*Uracentron flaviceps*, ♂, 123 mm SVL (KU 126781).

juvenile was obtained in October and has a snout-vent length of 60 mm. In Guyana, Beebe (1944:211) found a female with seven eggs in January and one with eight eggs in August.

Food.—In six stomachs the only exception to a variety of grasshoppers was one small beetle. In Guyana, Beebe (1944:210) found a cicada, ants, moths, berries, and seeds, in addition to beetles and orthopterans.

Uracentron flaviceps (Guichenot)

(FIGURE 121)

Material.—Lago Agrio, 1; Santa Cecilia, 1.

Identification.—This moderately large lizard with a short, depressed, spinous tail is unlike any other species in the area. The body and tail are black above and below. A narrow pinkish white collar is present; the head is pale orange with black flecks. Fugler and Schwaner (1968:253) noted that females have white or yellow flecks on the dorsal and ventral surfaces. ♂ 123+70 mm; ♀ 117+66 mm.

Occurrence.—Both specimens were taken from large trees after they were felled. Thus, the limited observations, supported by those of Fugler and Schwaner (1958:253), indicate that this species is arboreal in primary forest.

Life History.—Nothing is known.

Food.—One specimen contained many beetles.

SCINCIDAE

Mabuya mabouya (Lacépède)

(FIGURE 122)

Material.—Dureno, 9; Santa Cecilia, 35.

Identification.—This stocky-bodied skink is easily recognized by the presence of shiny smooth scales of uniform size on the dorsum. The species can be confused with only *Iphisa elegans*, a slender lizard having two longitudinal rows of greatly enlarged scales, both dorsally and ventrally. The dorsum of *Mabuya* is brown with a bronze sheen; the dark brown flanks are separated from the mid-dorsal color by a greenish bronze dorso-lateral stripe. The venter is greenish bronze, becoming pale blue on the tail. ♂ 94+132 mm; ♀ 100+139 mm.

Occurrence.—This heliophilic lizard is seldom found in forest, and when it has been found there, individuals usually were in areas of tree falls where sunlight reached the ground. The lizards were observed most frequently in clearings, banana groves, and at the forest edge; they forage on the ground and sun on logs or stumps.

Life History.—*Mabuya* gives birth to

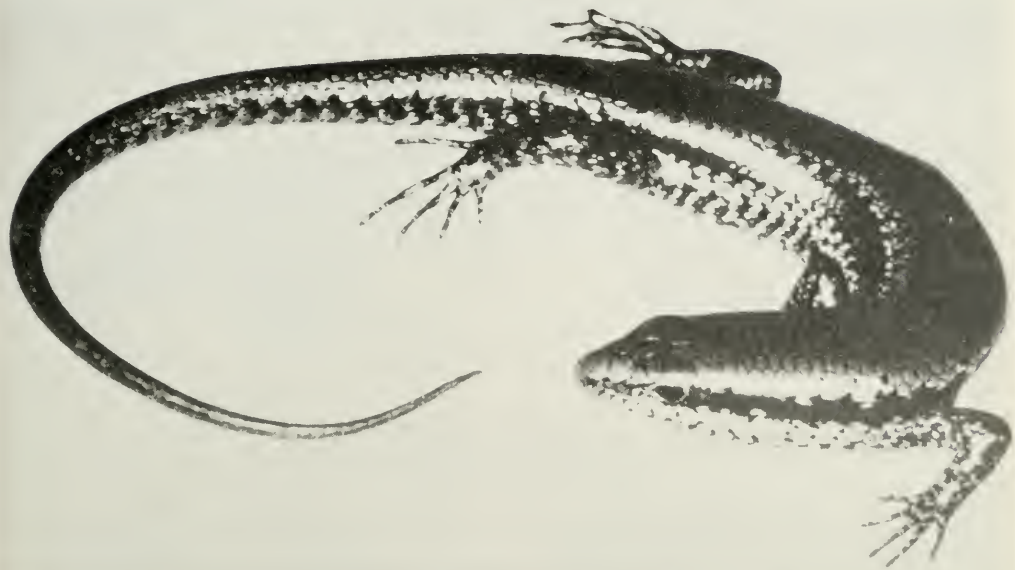


FIG. 122.—*Mabuya mabouya*, ♂, 94 mm SVL (KU 122127).

living young; females containing undeveloped ova were found in January through November. Ten females (March 2, June 2, and August 6) contained 4-6 ($\bar{x}=5.2$) well-developed embryos. The smallest female with developing embryos has a snout-vent length of 72 mm. The smallest juveniles have snout-vent lengths of 48 and 49 mm; they were obtained in October. The presence of ova in specimens collected through the year, possibly is indicative of acyclic breeding in the species.

Food.—In 29 stomachs, 66.3 percent of the volume was orthopterans; spiders comprised 13.8 percent, and the remainder was made up of six other groups of arthropods.

TEIIDAE

Alopoglossus atriventris Duellman

Alopoglossus atriventris Duellman, 1973, *Herpetologica* 29:228 [Type locality.—Lago Agrio, Provincia Napo, Ecuador].

Material.—Lago Agrio, 2.

Identification.—This small lizard is like *Alopoglossus copii* and *Leposoma*

parietale in having heavily keeled dorsal scales in oblique rows. *Alopoglossus atriventris* differs from both by having keeled ventral scales that are cream in juveniles and black in adult males, as opposed to smooth ventral scales that are cream (with black edges in some individuals of *A. copii*) or pale orange (males of *L. parietale*). Also, the head shields in *Alopoglossus atriventris* are slightly rugose, whereas they are keeled in *L. parietale* and smooth in *A. copii*. The dorsal surfaces of *A. atriventris* are silt brown; the sides of the body and tail are black with a white stripe extending from the corner of the mouth to the base of the hind limb. The ventral surfaces are cream in juveniles, cream with black edges to scales in females and subadult males, and black with white flecks in adult males. ♂ 51+84 mm.

Occurrence.—The two specimens were obtained in May while primary forest was being cleared by bulldozers. Data on specimens collected elsewhere indicate that this species inhabits the leaf litter in primary forest.

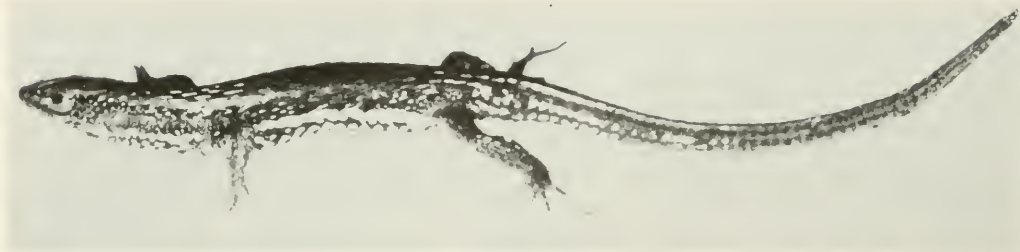


FIG. 123.—*Alopoglossus copii*, ♂, 51 mm SVL (KU 122138).

Life History.—No reproductive data are available; both males have seemingly fully developed testes.

Food.—The stomachs of both specimens were empty.

Remarks.—This species is known from several localities in the upper Amazon Basin in Colombia, Ecuador, and Perú; at some localities it occurs in sympatry with *Alopoglossus buckleyi* and at others with *A. copii*.

Alopoglossus copii Boulenger

(FIGURE 123)

Material.—Santa Cecilia, 22.

Identification.—This small lizard is like *Alopoglossus atriventris* and *Leposoma parietale* in having heavily keeled dorsal scales in oblique rows. *Alopoglossus copii* differs from both by having smooth, instead of heavily keeled, ventral scales. The head shields of *A. atriventris* have longitudinal ridges, and the head shields of *L. parietale* are keeled. In *A. copii* the venter is cream (with black edges on the scales in some large individuals). In *A. atriventris* the ventral coloration is the same, except that the venter is black in adult males; in *L. parietale* the venter is cream in females and pale orange in males. The dorsum of *A. copii* is dull brown with small, dark brown middorsal spots; the top of the head and sides of the body and tail are dark brown. A dull orange-tan dorsolateral stripe is evident on the anterior half of the body. The belly is yellowish cream, and the iris is dull red. ♂ 56+90 mm; ♀ 62+98 mm.

Occurrence.—This terrestrial lizard inhabits leaf litter in primary and secondary forest. Four individuals were found beneath logs on wet earth near a stream in a clearing, and another individual was sunning on a log in a clearing. Individuals have been found March through August; 75 percent of the specimens were obtained in June and July.

Life History.—Five gravid females having snout-vent lengths of 53-62 ($\bar{x}$ =58.0) mm obtained in June and July each contained two oviducal eggs 11.7 mm in length. One female laid two eggs on 26 June. The eggs were 13×9 mm and weighed 6 gm each. Two eggs of the same size and weight were found under a log on 22 June; they hatched on 13 August. The hatchlings had snout-vent lengths of 25 mm.

Food.—In 10 stomachs, spiders (47.0%), orthopterans (30.0%), and termites (11.0%) comprised the bulk of the food. Sow bugs (8.0%) and caterpillars (4.0%) comprised the remainder.

Ameiva ameiva petersii Cope

(FIGURE 124)

Material.—Puerto Libre, 6; Santa Cecilia, 333.

Identification.—This moderate-sized lizard with a long tail can be confused only with *Kentropyx pelviceps*. The latter has small, keeled ventral scales and rugose head shields, whereas *Ameiva* has large smooth ventral scales in eight longitudinal rows and smooth head shields. *Kentropyx* has a broad middorsal bright green stripe beginning on the head and



FIG. 124.—*Ameiva ameiva petersi*. Upper: ♂, 128 mm SVL (KU 109698). Lower: ♀, 103 mm SVL (KU 109695).

changing to tan or reddish brown posteriorly. Adult male *Ameiva* are green posterodorsally. Females and immature males are brown with cream stripes and spots. This coloration resembles that of *Tupinambis tequixin*, which is black with creamy spots. In *Tupinambis* the smooth ventrals are in 20 or more longitudinal rows, and the dorsal scales are granular.

Adult males are brilliantly colored. The top of the head is olive-gray; the thoracic region and forearms are brown or reddish brown. The rest of the dorsum is green with two lateral brown stripes separated from one another and from the dorsal green color by rows of greenish yellow spots. The tail is brown

above and laterally; the hind limbs are green with small blue spots. The chin is white or pale orange. The belly is bluish white, dark blue laterally. Adult females have an olive-brown head and pale brown dorsum, limbs and tail. A dorsolateral and lateral creamy yellow stripe borders a dark brown lateral band. In some individuals the stripes, especially the dorsolateral one, are fragmented into spots. The stripes continue onto the base of the tail. The ventral surfaces are grayish white. Juveniles are colored like females, except that the middorsal area is marked by three longitudinal rows of tan spots. ♂ 142+303 mm; ♀ 125+215 mm.

Occurrence.—This active, heliophilic

lizard primarily inhabits clearings, where individuals usually are seen only on sunny days or when the air temperature exceeds 26°C. On warm days individuals were seen even in light rain. Field notes on 312 specimens reveal the following sites of capture: clearings (175), sand bar of island in river (119), forest edge (14), and secondary forest (4). Three were found beneath logs in clearings on cool cloudy days.

Fitch (1968:36) reported body temperatures of 38 *Ameiva ameiva petersii* from Santa Cecilia in March 1967. He found body temperatures of 34.0-40.0°C ($\bar{x}=37.0\pm0.27$) and deviation from air temperatures of +3.8-11.6°C ($\bar{x}=6.86\pm0.33$). Temperature data were recorded for an additional 22 individuals in November and December 1971: body 34.7-39.0 ($\bar{x}=37.3$), air 26.5-32.4 ($\bar{x}=29.6$), deviation of body from air +4.2-12.1 ($\bar{x}=7.76$)°C.

Life History.—*Ameiva ameiva* is the only lizard at Santa Cecilia for which a seasonal reproductive cycle apparently can be demonstrated (Simmons, 1975). Ninety-three adult females are available from throughout the year, except January. Females having oviducal eggs were found in July (3), August (2), October (1), November (2), and December (1). Mature ovarian eggs were found in one female from May and two from July. Mating was observed on 29 June. Simmons observed females digging nests in the sand bar on the island on 11 November and 12 December and found a clutch of four eggs on 3 December. The eggs (19-22 $\times$ 12 mm) hatched 140 days later on 22 April. Clutch sizes based on numbers of oviducal and mature ovarian eggs are 2-6 ($\bar{x}=3.7$, $N=12$). The hatchlings from the clutch raised had snout-vent lengths of 39-41 mm. Juveniles having snout-vent lengths of 39-41 mm were found in March (15), April (1), November (3), and December (6). No *Ameiva* were obtained in January, and only six were collected in February, of

which one was a juvenile having a snout-vent length of 51 mm.

These data and the seasonal development of the fat bodies in females (Simmons, 1975) seem to demonstrate that at Santa Cecilia *Ameiva ameiva* has a cyclic breeding season lasting about six months; eggs mature in July through December, and young hatch in October through April.

Food.—Examination of the stomach contents of 106 individuals revealed that *Ameiva ameiva* is a general opportunistic feeder (Table 7). As a group, orthopterans were the most common food items eaten; these included a variety of grasshoppers, crickets, and roaches, and mole crickets (Gryllotalpidae). Caterpillars are abundant in cleared areas, and these comprised the second most common food item in *Ameiva*. Six individuals contained only maggots. These lizards were collected on the island in the Río Aguarico, where fly-blown fish are not uncommon on the shore. One individual contained an adult gecko (*Gonatodes conchinnatus*); another contained the tail of a skink (*Mabuya mabouya*), and one contained two small lizard eggs.

Remarks.—At the time of our first field work at Santa Cecilia in November 1966, *Ameiva* was observed only along the banks of the Río Aguarico and on the island in the river. As more land was cleared, *Ameiva* expanded its range, following trails, roads, and cultivated land. Apparently, without the aid of human activity in clearing land, *Ameiva* follows major river courses, where sand banks and associated seral vegetation provide suitable non-forest habitat. Thus, *Ameiva* probably reached Puerto Libre by following the Río Aguarico. In May 1969, when primary forest was being cleared at Lago Agrio, no *Ameiva* was found. At that time Lago Agrio was separated from the Río Aguarico by about 3 km of primary forest. In 1971-72 Lago Agrio was connected by road to Santa Cecilia and the Río Aguarico; many *Ameiva* were observed at Lago Agrio.



FIG. 125.—*Arthrosaura reticulata*, ♀, 70 mm SVL (KU 109823).

The clearing of land at Santa Cecilia has resulted in the creation of at least marginal habitat for two species that originally were ecologically exclusive — *Ameiva ameiva petersii* and *Kentropyx pelviceps*. The ecological relationships of the two species are discussed in the account of the latter species.

***Arthrosaura reticulata* (O'Shaughnessy)**

(FIGURE 125)

Material.—Lago Agrio, 1; Santa Cecilia, 8.

Identification.—This dull brown microteiid has the scales on the body arranged in transverse rows; the scales on the dorsum of the body are strongly keeled and pointed posteriorly, and the posterior tips of the scales overlap the scales in the following row. The dorsal scales are separated from the ventral plates, which have rounded posterior margins, by one or two rows of small, granular scales. *Prionodactylus argulus* and *P. manicatus* differ from *Arthrosaura* by having 8-12 rows of granular scales between the dorsals and ventrals. *Arthrosaura reticulata* is most easily confused with *Ptychoglossus brevifrontalis*, in which the dorsal scales have low rounded keels not projecting posteriorly and non-overlapping scales in the following row. Furthermore, *Arthrosaura* has three supraoculars and anterior chinshields that are larger than the second pair of chinshields, whereas *Ptychoglossus* has four supraoculars and anterior chinshields

that are shorter than the second pair of chinshields.

The dorsum is dark reddish brown. In small individuals there are six rows (paravertebral, dorsolateral, and lateral) of small black spots with brown centers; the dorsolateral rows continue onto the tail. In some larger individuals the spots are not discrete, and the pattern consists of irregular black flecks on the dorsum. The lips are barred black and tan; the chin and throat are cream with dark brown or black spots laterally. In juveniles and females the belly is cream; in adult males it is salmon. The entire tail is orange in juveniles, but in adults only the ventral caudal surface is orange; the dorsum is brown. The iris is orange-brown. ♂ 61+109 mm; ♀ 70+125 mm.

Occurrence.—All individuals were found amidst leaf litter on the ground in primary forest by day, save one, which apparently was frightened from shelter in leaf litter at night.

Life History.—Two females (one from June and one from August) each contained two oviducal eggs 13.0 and 13.6 mm in length.

Food.—In six stomachs, sow bugs formed 33.3 percent and mole crickets 31.7 percent of the volume. Beetles and roaches were the other identifiable items.

***Bachia trinasale trinasale* (Cope)**

(FIGURE 126)

Ophiognomon trinasale Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 1868:100 [Type locality.—Napo or Alto Marañón, Ecuador].

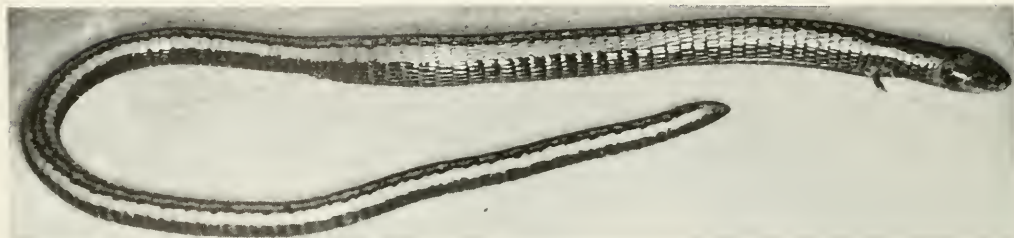


FIG. 126.—*Bachia trinasale trinasale*, ♀, 79 mm SVL (KU 122195).

Bachia trinasale trinasale—Dixon, 1973, Misc. Publ. Mus. Nat. Hist. Univ. Kansas 57:29.

Material.—Lago Agrio, 21; Puerto Libre, 2; Santa Cecilia, 1.

Identification.—This slender lizard differs from all others in the area by having small forelimbs and hind limbs that are reduced to small stubs. The dorsal surfaces of the body and tail are orange tan; the head, flanks, and dorsal stripes are dark brown, and the venter is dull brown. ♂ 72+85 mm; ♀ 79+120 mm.

Occurrence.—The two specimens from Puerto Libre were obtained in July; one was dug out of sandy soil, and the other was found in a trench. Both were in secondary forest near the Río Aguarico. The single specimen from Santa Cecilia was obtained in May from under a rotting log in a clearing. All of the material from Lago Agrio was obtained between 28 April and 4 June 1969. The lizards were unearthed by bulldozers clearing primary forest. The soil in which those were found at Puerto Libre is sandy, but the soil at Santa Cecilia and Lago Agrio is lateritic. Individuals were not observed in undisturbed forest at Lago Agrio; presumably the lizards are active in the soil or at least under the leaf litter.

Life History.—Both specimens from Puerto Libre are mature females; one obtained on 6 July contained two oviducal eggs 12.9 mm in length, and one obtained on 9 July contained two large ovarian eggs 9.1 mm in length. No juveniles were found.

Food.—Six individuals contained

beetle larvae; four contained earthworms, and one contained a centipede.

Remarks.—The variation in, and distribution of, *Bachia trinasale*, which is known only from the Amazon Basin in Ecuador and Perú, were discussed in detail by Dixon (1973).

Dracaena guianensis Daudin

(FIGURE 127)

Material.—Santa Cecilia, 3.

Identification.—This large lizard with a blunt head resembles a crocodile with a short snout. The dorsal scales are small with large conical scales arranged in paravertebral and diagonal lateral rows on the body, and several rows on the tail, of which the dorsolateral rows are the most prominent. The only other lizard of equal size in the area, *Tupinambis tequixín*, has uniformly small dorsal scales, a long snout, and entirely different coloration. The dorsum of *Dracaena guianensis* is dull brown or grayish brown with irregular, yellowish tan spots on the flanks. In adult males the throat is mottled orange and black, and the belly is yellowish brown; in adult females the ventral surfaces are gray. The scales around the eye are orange or red, and the iris is dull brown. ♂ 371 mm; ♀ 412 mm.

Occurrence.—The three specimens came from near the banks of the Río Aguarico. Two other individuals were observed on the ground near the river; one of these took refuge in a hole in the river bank.

Life History.—No data are available.

Food.—*Dracaena* feeds on gastro-



FIG. 127.—*Dracaena guianensis*, ♂, 293 mm SVL: Limoncocha, Provincia Napo, Ecuador (KU 122171).

pod; it crushes the shells with the large flattened teeth and spits out the fragments of the shells (Conant, 1955; Vanzolini 1961). No specimens from Santa Cecilia contained food in their stomachs.

Iphisa elegans Gray

(FIGURE 128)

Material.—Lago Agrio, 2; Puerto Libre, 1; Santa Cecilia, 4.

Identification.—This slender lizard with large, smooth scales can be confused only with *Mabuya mabouya*. In the latter species all of the scales on the body are approximately the same size, but *Iphisa* has two longitudinal rows of greatly enlarged scales both dorsally and ventrally. The head and body are brown with orange-tan dorsolateral stripes; the flanks are dark brown. The tail is gray in juveniles and brown in adults. The venter is gray in juveniles, creamy gray in adult females, and salmon pink in adult males. ♂ 58+93 mm; ♀ 54+93 mm.

Occurrence.—All individuals were found amidst leaf litter on the forest floor, except one, which was under a log. One was in secondary forest; the others were in primary forest.

Life History.—One female obtained in August contained two ovarian eggs.

Food.—One individual had eaten a roach.

Remarks.—Fitch (1968:37) reported the body temperature of this species as 28.2°C; he erroneously used the name *Calliscincophis agilis*.

Kentropyx pelviceps Cope

(FIGURE 129)

Material.—Dureno, 2; Lago Agrio, 2; Puerto Libre, 2; Santa Cecilia, 134.

Identification.—This moderate-sized lizard with a long tail can be confused only with *Ameiva ameiva petersii*. The latter has large, smooth ventral scales and smooth head shields, whereas *Kentropyx pelviceps* has small, keeled ventral scales and rugose head shields. Fur-



FIG. 128.—*Iphisa elegans*, ♂, 51 mm SVL (KU 122172).



FIG. 129.—*Kentropyx pelviceps*, juvenile, 50 mm SVL (KU 122181).

thermore, *Kentropyx* is the only lizard in the area having a broad middorsal bright green stripe beginning on the head and continuing to the midlength of the body, where it changes to reddish brown or tan.

Adult males are brightly colored, and in addition to the middorsal stripe, they have a brown head and limbs with tan flecks on the latter. Bordering the middorsal stripe is an irregular dark brown stripe expanded laterally to form short, transverse bars extending midway onto the flanks, which otherwise are marked by small, pale blue spots. The throat and chest are grayish white; posteriorly, this blends into salmon-orange on the belly and ventral surfaces of the limbs. Adult females usually have a broad, dark brown field on either side of the mid-

dorsal stripe, which is greenish tan. The dark brown field is not so distinctly broken into bars as in males, and the lower flanks are uniform brown. The venter is pale gray. Juveniles are bronzetan with a pale green middorsal stripe bordered by dark brown. A greenish yellow stripe extends from the eye, above the ear opening, and onto the flanks, where it persists as a series of faint dashes in half-grown individuals. ♂ 115 + 244 mm; ♀ 116 + 209 mm.

Occurrence.—*Kentropyx pelviceps* is a diurnal inhabitant of forest, where it usually is found in patches of sunlight on the forest floor. Individuals have been observed actively foraging amidst leaf litter, on logs, around bases of trees, and to heights of 3 m in tangled vegetation. Only one was taken in a large man-made

clearing, although natural small clearings, such as those created by tree falls, commonly are inhabited by this lizard. Nearly equal numbers (48 and 53) were found in primary and secondary forest; five each came from a banana grove and forest edge. Inactive individuals were found beneath logs in the forest by day, and one juvenile was sleeping on a bush about 1 m above the ground at night.

Fitch (1968:36) reported on body temperatures of 36 specimens from Santa Cecilia; the temperatures were 31.0-40.3°C ($\bar{x}=35.75\pm0.39$) with a deviation of $+6.95\pm0.44^\circ\text{C}$ from air temperatures. The heliophilic behavior of this lizard precludes activity on cloudy or rainy days.

Life History.—Despite the large sample size, few egg-bearing females were obtained. The smallest female containing ovarian eggs has a snout-vent length of 91 mm. Twenty-three females collected in March through November contained immature ovarian eggs. One female from May contained five oviducal eggs 20.1 mm in length; two from March contained four and six large ovarian eggs. Four adherent eggs were found in a cavity in a bamboo about 1 m above the ground on 8 May; the eggs were about 23 mm in length and hatched on 18 May. The hatchlings had snout-vent lengths of 38-40 mm. Juveniles having snout-vent lengths of 35-43 mm were found in March, May, June, October, and November.

Although the reproductive data are inconclusive, the presence of ovarian eggs and hatchlings from March through November indicates that some eggs also must hatch in January. Adult females are absent from our collections made in December through February, but the above data suggest that reproduction occurs throughout the year.

Food.—Examination of 84 stomachs revealed that orthopterans constitute about two-thirds of the volume of food eaten. Of these, one-third are roaches

TABLE 7.—Comparative Food Analysis of *Ameiva ameiva* and *Kentropyx pelviceps*.
(Percent frequency of occurrence of prey/percent volume.)

FOOD	<i>Ameiva ameiva</i> (N=106)	<i>Kentropyx pelviceps</i> (N=84)
Isopoda	4.0/6.8	-----
Arachnida	6.3/3.5	17.8/13.4
Coleoptera	7.0/6.0	0.7/0.1
Dermaptera	3.3/2.5	-----
Diptera (larvae)	3.0/5.7	-----
Hemiptera	13.4/4.9	-----
Lepidoptera (larvae) ..	17.3/20.5	0.7/0.8
Orthoptera	31.3/33.3	65.7/62.3
Misc. Insecta	11.9/21.9	13.7/21.9
Amphibia (Anura)	-----	0.7/10.7
Reptilia (Sauria)	2.6/0.9	0.7/0.8

and the others grasshoppers and crickets. Spiders make up about 18 percent of the volume (Table 7). One individual contained a frog (*Eleutherodactylus ockendeni*) and one a lizard (*Anolis trachyderma*).

Remarks.—At the beginning of our field studies at Santa Cecilia in 1966, *Kentropyx pelviceps* and *Ameiva ameiva petersii* were ecologically exclusive; the latter was found only along the edge of the Río Aguarico and the airstrip, whereas *Kentropyx* was confined to primary forest. With continued human disturbance of the forest, habitats at least marginally suitable for both species were created. Consequently, it is now possible to find the species together in partially cleared forest and in banana groves. Optimal habitat for *Kentropyx* is receding, while optimal habitat for *Ameiva* is increasing. No interactions between the species have been observed. Both feed heavily on orthopterans, but the abundance of these insects, especially in partially cleared forest, probably precludes competition for food.

Leposoma parietale (Cope)

(FIGURE 130)



FIG. 130.—*Leposoma parietale*, ♂, 34 mm SVL (KU 112209).

Material.—Lago Agrio, 2; Puerto Libre, 28; Puerto Ore, 1; Santa Cecilia, 83.

Identification.—This small lizard resembles *Alopoglossus atriventris* and *A. copii* in having heavily keeled dorsal scales in oblique rows. It differs from both by having keeled dorsal head scales. The head scales of *Alopoglossus copii* are smooth, and those of *A. atriventris* have low longitudinal ridges. The ventral scales of *L. parietale* and *A. copii* are smooth, whereas those of *A. atriventris* are heavily keeled. The dorsum is dull reddish brown; the head and sides of the body are dark brown. A pale tan dorso-lateral stripe is evident on the anterior half of the body in most specimens. In females the chin is white, and the belly is cream; in males the chin and belly are orange. The iris is orange-tan. ♂ 38+55 mm; ♀ 39+55 mm.

Occurrence.—*Leposoma parietale* is active by day amidst leaf litter on the forest floor. Sixty-two percent of the specimens were found in primary forest; the remainder was about equally divided among secondary forest, forest edge, and clearings. Most individuals were active on sunny days; the lizards forage in the leaf litter and sun on the litter or small logs. A pile of wood chips at the base of a stump at the forest edge harbored a large population. Two individuals were found moving on the ground at night—one in a clearing and one in secondary forest; presumably both were frightened from their nocturnal refuges by the observers.

Life History.—Females produce two eggs at a time; the largest oviducal eggs

are 8 mm in length. Twelve females with oviducal eggs were obtained in March, June, July, and August. Ten others from July and August have immature ovarian eggs, and three from June and July show no evidence of reproductive activity. The limited data indicate that perhaps reproduction in *Leposoma parietale* is cyclic.

Food.—A large variety of small insects are eaten. In 38 stomachs, ants and hemipterans each accounted for 21.4 percent of the volume. Spiders and sow bugs each amounted to less than 6 percent, whereas small orthopterans comprised 14.6 percent. One individual contained the head of a juvenile *Leposoma*.

Neusticurus ecpleopus Cope

(FIGURE 131)

Material.—Lago Agrio, 5; Puerto Ore, 1; Santa Cecilia, 71.

Identification.—This small lizard has the appearance of a minute, short-headed crocodilian. The snout is pointed, and the dorsal scutellation consists of small scales with four longitudinal rows of enlarged keeled scales forming four ridges on the back and two on the tail. Other similarly colored small lizards in the area are *Leposoma parietale*, *Alopoglossus atriventris*, and *A. copii*, but these have uniformly large, keeled scales on the body. *Dracaena guianensis* and *Thecadactylus rapicauda* are the only other lizards in the area that have large scales mixed with small ones on the dorsum. *Thecadactylus* has small, granular scales on the head, a short thick tail, and broadly expanded toes, whereas *Neusticurus* has large plates on the top of the head, a slender tail, and slender toes. *Dracaena*

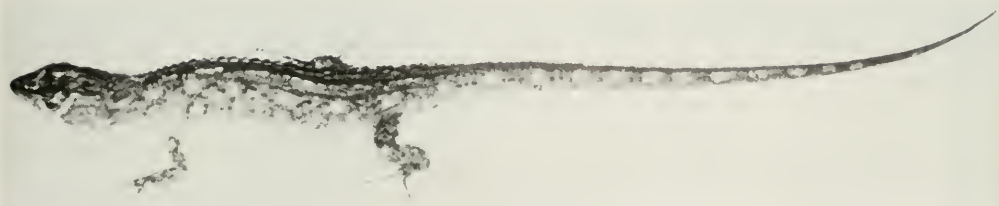


FIG. 131.—*Neusticurus ecpleopus*, ♀, 65 mm SVL (KU 126807).

has a large, blunt head and scattered large scales amidst small scales on the dorsum.

Adult *Neusticurus ecpleopus* are dull brown above with the flanks more olive-brown. Faint quadrangular tan spots are arranged in alternating rows on the dorsum. In females there is a single black spot with a cream center above the insertion of the arm; males have three additional spots – one on the neck and two on the flanks. The belly is cream (with rusty brown edges on the scales in larger individuals). The labials and chin are pale yellow in some individuals and are marked by brown or black diagonal bars. In juveniles the dorsum is pinkish tan; the head and flanks are dark brown, and the throat and belly are black and white. ♂ 64+112 mm; ♀ 67+101 mm.

Occurrence.—*Neusticurus ecpleopus* seems to be restricted to the immediate vicinity of small streams. All individuals were found within 1 m of water. The lizards always were associated with wet ground and active amidst leaf litter at the edge of the water. Some were under logs at the edge of the water. When disturbed, the lizards readily entered water and sought refuge under detritus on the bottom of the stream. One was observed in the water at night, but probably it inadvertently had been displaced from its nocturnal retreat. Only two individuals were found in clearings; all others were in forest. The lizards were associated only with small rivulets, usually less than 1 m wide and only a few cm deep; most such streams where *Neusticurus* were found had a good current and

sandy bottoms. Except for the two specimens found in clearings, all were in heavy shade.

Fitch (1968:37) reported body temperatures of 15 individuals as 24.5–30.4°C ($\bar{x}=26.8\pm0.51$) with the mean deviation from air temperature being $+0.66\pm0.34^\circ\text{C}$. All of our specimens were obtained in March through August. Most (42 specimens) were obtained through the diligent efforts of Henry S. Fitch in March 1967. Because no specific attempt was made to collect these lizards other than in March and June, their absence in collections made in September through February probably more accurately reflects the nature of collecting than seasonality of the lizards.

Life History.—Two females (one from March and one from April) each contained two oviducal eggs 11 mm in length. Juveniles, presumably recent hatchlings, having snout-vent lengths of 23–25 mm were found in March, June, and July. Thus, the species apparently has a long breeding season, if indeed it does not reproduce throughout the year. Sherbrooke (1975) demonstrated breeding throughout the year in this species at Tingo María, Perú.

Food.—Examination of 25 stomachs revealed a diversity of food items, of which orthopterans (30.8% volume) were the most numerous, followed by spiders (19.7%), ants (14.4%), and beetle larvae (10.0%). One contained a centipede, and three contained lizards – *Anolis trachyderma*, *Leposoma parietale*, and *Neusticurus ecpleopus*.

Remarks.—Despite the similarity in

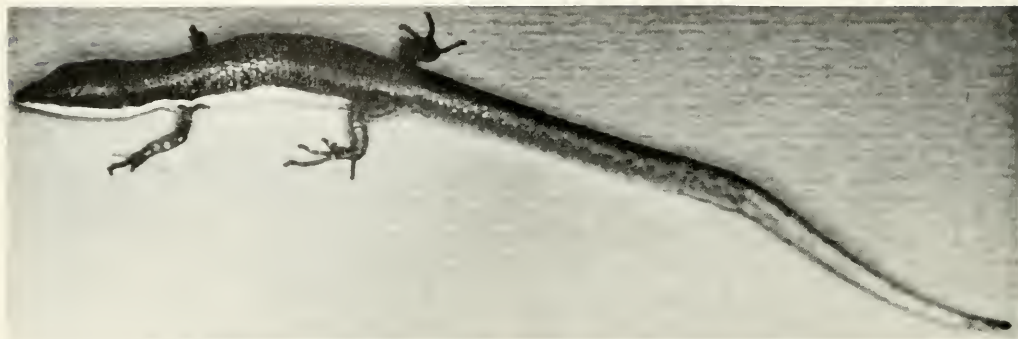


FIG. 132.—*Prionodactylus argulus*, ♂, 35 mm SVL (KU 126834).

habits, size, and coloration of *Neusticurus ecpleopus* and *Echinosaura horrida*, the former, unlike the latter, does not become rigid when handled, turn over, nor wrap its tail around objects, as described by Uzzell (1965:89), and Leviton and Anderson (1966:160). When handled, *Neusticurus ecpleopus* writhes strenuously and bites ferociously.

Prionodactylus argulus (Peters)

(FIGURE 132)

Material.—Lago Agrio, 12; Puerto Libre, 4; Santa Cecilia, 44.

Identification.—This small microteiid has keeled dorsal scales in transverse rows; the dorsal scales are separated from the ventrals by a zone of 8-12 small, granular scales. The broad zone of lateral granules immediately distinguishes this species from all other lizards in the area, except *Prionodactylus manicatus*, which has one frontonasal scale (two in *P. argulus*). Furthermore, the larger *P. manicatus* has uniform dark brown flanks and a white ventrolateral stripe extending from the lip to the hind limb; *P. argulus* has brown or reddish brown flanks with black ocelli with cream centers.

The dorsal surfaces of the head and body are brown to olive-brown, becoming paler posteriorly and changing to reddish tan or orange on the tail; the darker anterior coloration continues pos-

teriorly on the body as a series of dashes or narrow longitudinal lines. The dorsal surfaces of the limbs are tan to orange with yellow spots. A dorsolateral tan stripe extends the length of the body. The flanks are orange-tan to reddish brown with a row of black ocelli with white to yellow centers. The lips are pinkish white to creamy yellow; a ventrolateral stripe of the same color continues posteriorly on the body, bordered below by a tan stripe in some specimens and blending with the venter in others. The chin, throat, and belly are metallic yellow, and the underside of the tail is orange. The iris is bronze. ♂ 43+98 mm; ♀ 47+94 mm.

Occurrence.—Although *Prionodactylus* is principally a terrestrial inhabitant of primary forest, where the majority of individuals were observed moving about in leaf litter by day, the species does occur elsewhere. Ten were obtained in secondary forest, and three each in clearings and banana groves. Three individuals were observed sunning on logs, but most were in the shade. Two were observed on buttresses of trees; one was on the branch of a bush, and two juveniles were on herbaceous plants. Ten were sleeping at night on leaves and stems of herbs and bushes; all were at heights of less than 1.5 m, except one on a *Heliconia* leaf about 2 m above water in a swamp.

Life History.—All females were ob-

tained in March through September; some individuals in each of these months, except April, contained small ovarian eggs. Four females from July contained oviducal eggs 8.9-9.2 ($\bar{x}$ =9.06) mm in length; three had two eggs and one had one egg. The presence of small juveniles at various times of the year suggests a more lengthy breeding season than do the data from gravid females. The seven smallest juveniles have snout-vent lengths of 18-21 ($\bar{x}$ =20.0) mm; these were found in January (1), July (3), September (1), and December (2).

Food.—In the 20 stomachs examined, spiders were the most frequent food item (46.0% frequency, 36.2% volume), followed by orthopterans (27.0% and 30.0%). Ants, hemipterans, beetle larvae, and sow bugs comprised the rest of the identifiable remains.

Remarks.—The limited data on the diurnal activity of this species in bushes and other vegetation above the ground are supported by the presence of individuals in the stomach of the diurnal arboreal snake *Oxybelis argenteus*. Fitch (1968:38) commented on the body temperatures of the species under the name *Prionodactylus oshaughnessyi*. He noted a body temperature of 28.8°C and air temperature of 26.7°C.

Prionodactylus manicatus
(O'Shaughnessy)

(FIGURE 133)

Material.—Lago Agrio, 1; Puerto Libre, 5; Santa Cecilia, 18.

Identification.—This moderately small microteiid has keeled dorsal scales in transverse rows. The dorsal scales are separated from the ventral scales by a zone of 8-12 granular scales. The broad zone of granular scales distinguishes this lizard from all others in the area, except *Prionodactylus argulus*, which has two frontonasal scales (one in *P. manicatus*). Furthermore, the smaller *P. argulus* has brown or reddish brown flanks with black ocelli with cream centers; *P. manicatus* has uniform dark brown flanks and



FIG. 133.—*Prionodactylus manicatus*, hatchling, 26 mm SVL (KU 122196).

a white ventrolateral stripe extending from the lip to the hind limb.

The dorsum is dull olive-brown or brown with or without two rows of irregular dark brown spots; a bronze dorsolateral stripe extends from the orbit to the base of the tail. The flanks are dark brown, and the sides of the head are darker brown or black. A light labial stripe continues posteriorly on the ventrolateral surface of the flank to the base of the hind limb. The stripe is white or yellowish white anteriorly and golden yellow or bronze posteriorly. The chin and throat are iridescent white, and the undersides of the forelimbs and the belly are iridescent yellow. The ventral surfaces of the hind limbs and tail are orange. In juveniles the dorsum is dull brown, and the tail is rusty orange; the forelimbs are white, and the belly is creamy yellow. ♂ 65+93 mm; ♀ 70+99 mm.

Occurrence.—All specimens were in, or at the edge of, primary forest. One was 35 cm above the ground on the stem of a small bush; one was sunning on the base of a stilt palm, and two were sunning on logs. Most of the others were moving about amidst leaf litter. Several were observed to take shelter in the roots of stilt palms. About one-third of the specimens collected and more than half of those seen, but not collected, were in sunlight.

Life History.—One female collected in March contained two oviducal eggs



FIG. 134.—*Ptychoglossus brevifrontalis*, ♀, 58 mm SVL (KU 122197).

15.0 mm in length. A female from March and one from May contained small ovarian eggs, and another from March showed no evidence of reproductive activity. An egg found beneath a log on 8 July hatched the following day; the hatchling had a snout-vent length of 26 mm. Eight other juveniles have snout-vent lengths of 27-33 ($\bar{x}$ =28.9) mm and were collected in May (1), July (6), and August (1).

Food.—Identifiable remains in 11 stomachs consisted of spiders (47.6% frequency, 59.5% volume) and orthopterans (42.8% and 22.3%).

Remarks.—Although, in comparison with *Prionodactylus argulus*, this species seems to be restricted to primary forest, it is heliophilic; most *P. argulus* were found in shade.

***Ptychoglossus brevifrontalis* Boulenger**

(FIGURE 134)

Material.—Puerto Libre, 1; Santa Cecilia, 1.

Identification.—This long, slender microteiid has the scales on the body arranged in transverse rows; the scales on the dorsal surface of the body have low, rounded keels with straight posterior margins. The dorsals are partially separated from the ventrals by one incomplete row of granular scales. The ventrals are smooth and have straight posterior margins. The dorsals are partially separated from the ventrals by one incomplete row of granular scales. The ventrals are smooth and have straight posterior margins. Among other micro-

teiids having transverse rows of scales on the body, *Bachia trinasale* has the hind limbs reduced to small stubs and *Prionodactylus argulus* and *P. manicatus* have 8-12 rows of granular scales laterally separating strongly keeled dorsals from the ventrals. *Ptychoglossus brevifrontalis* is most easily confused with *Arthrosaura reticulata*, in which the dorsal scales are strongly keeled with pointed posterior margins overlapping scales in the following row and the ventral plates have rounded posterior margins. Furthermore, *Ptychoglossus* has four supraoculars and anterior chinshields that are shorter than the second pair of chinshields, whereas *Arthrosaura* has three supraoculars and anterior chinshields that are longer than the second pair of chinshields.

In adult females, the dorsum is reddish brown with a faint orange-tan dorsolateral stripe and dark brown flanks. The lips are cream with brown bars; small cream spots are present on the sides of the neck. The chin is white with large, brown spots laterally. The chest is yellow, becoming orange posteriorly. The ventral surface of the tail is pinkish white. The iris is reddish brown. ♀ 59+93 mm.

Occurrence.—One was found beneath a stone at the edge of the forest, and another was amidst leaf litter in primary forest.

Life History.—A female obtained in August contained two oviducal eggs 10.5 mm in length, and one found in July had two ovarian eggs.



FIG. 135.—*Tupinambis tequixin*, ♂, 292 mm SVL; Belém, Estado do Pará, Brasil (KU 128264).

Food.—Both individuals lacked food in the stomachs.

Taxonomic Comments.—*Ptychoglossus nicefori* was diagnosed by Loveridge (1929) and Dunn (1944) as having 32 transverse rows of dorsal scales and lacking dorsolateral stripes, as opposed to *P. brevifrontalis*, which has 34 rows of scales and a dorsolateral light stripe. Of the two specimens from Puerto Libre and Santa Cecilia, one has 32 and the other 31 rows of scales. The faint dorsolateral stripe evident in life is not visible in preservative. On the advice of James R. Dixon, I refer our specimens to *Ptychoglossus brevifrontalis*; *P. nicefori* (Loveridge) is considered to be a junior synonym.

Tupinambis tequixin (Linnaeus)

(FIGURE 135)

Material.—Santa Cecilia, 2.

Identification.—This is the largest lizard in the area. It has small, flat dorsal scales and 20 or more longitudinal rows of larger, smooth scales on the belly. The dorsum is black with small pale creamy white spots dorsolaterally and tan flecks overall. The adults, because of their size, can be confused only with *Draconia guianensis* — a large, brown lizard having large conical scales interspersed among small granular scales on the dorsum. Juveniles of *Tupinambis* might be confused with *Ameiva ameiva* and *Kentropyx pelviceps*; the latter has keeled ventral scales, and *Ameiva* has smooth ventrals in eight longitudinal rows. Both

species have small, granular dorsal scales — round in *Ameiva* and keeled in *Kentropyx*. The only adult from Santa Cecilia is a female having a snout-vent length of 307 mm, but adults of this species are known to reach snout-vent lengths in excess of 400 mm.

Occurrence.—Although this large lizard sometimes is seen in the forest, most individuals have been observed in clearings, where they forage around clumps of brush and sun on logs.

Life History.—A female obtained in February contained three ovarian eggs 33.7 mm in length. Beebe (1945:26) found clutches of *Tupinambis* eggs in termite nests in Guyana.

Food.—One individual contained a caterpillar and a grasshopper. Beebe (1945:25) in reporting on the species in Guyana stated: "The tegu is an omnivorous feeder in the widest possible meaning of that term. No phylum of animals is refused, whether the organisms are small or large, living or long dead. A large number of plants, leaves and berries are taken." In light of these statements, the food data from Santa Cecilia must be taken only for what they are — contents of one stomach.

Taxonomic Comments.—I follow Presch (1973:741) in placing *Tupinambis nigropunctatus* Spix, 1825, in the synonymy of *T. tequixin* (Linnaeus, 1758).

Remarks.—During early field work at Santa Cecilia (1966-68), this large lizard rarely was seen; perhaps one was observed each month or so. With increased

clearing of the forest, the lizards either have become more numerous or at least more easily observed. On sunny days in 1971-72 *Tupinambis* was readily observed in clearings and partly cut-over areas; as many as five could be seen in one morning.

AMPHISBAENIANS

AMPHISBAENIDAE

Amphisbaena fuliginosa Linnaeus

Material.—Lago Agrio, 3; Santa Cecilia, 3.

Identification.—This amphisbaenian is easily distinguished from all other lizards by the complete absence of limbs, short blunt tail, non-imbricate scales of uniform size arranged in transverse rows around the body, and the eye covered by a large scale. The last two characters distinguish *Amphisbaena* from snakes. These reptiles are dull grayish white above and below, with a slight pinkish tint in some specimens; the markings consist of black transverse bars irregularly arranged, usually offset dorsally and less conspicuous ventrally. ♂ 310 mm; ♀ 367 mm.

Occurrence.—Individuals have been observed by natives on the forest floor by day. Three specimens were unearthed by bulldozers at Lago Agrio; one of these was in the roots of a stilt palm.

Life History.—No reproductive data are available. The smallest juveniles, having snout-vent lengths of 204 and 211 mm, were obtained in June and July, respectively.

Food.—Three individuals contained food: one a centipede, one an earthworm, and one ants.

Taxonomic Comments.—Vanzolini (1951) recognized five subspecies of *Amphisbaena fuliginosa*; these were defined primarily on coloration (head spotted or not, venter as densely pigmented as the dorsum, and arrangement of the dorsal markings). In the specimens from Lago Agrio and Santa Cecilia, the head is spotted in two, immaculate in four;

the venter is much less densely pigmented than the dorsum in three; the dorsal spots form a checker-board pattern in five and transverse bars in one. These specimens seem to possess characters found in three subspecies — *amazonica* to the east, *bassleri* to the south, and *varia* to the north. With such variation in the small sample at hand, it is futile to recognize subspecies in the area.

SNAKES

ANILIIDAE

Anilius scytale (Linnaeus)

(PLATE 4)

Material.—Lago Agrio, 4; Santa Cecilia, 3.

Identification.—This cylindrical snake has a short, blunt head and tail; the ventral scutes are only slightly wider than the dorsal scales. The small eye is beneath a single large scale, and there are only five enlarged plates on the top of the head. In these characters, *Anilius scytale* differs from all other snakes in the area. The coloration of red and black rings resembles patterns of *Micrurus langsdorffi*, *Atractus elaps*, and *Oxyrhopus melanogenys*, but all of these have enlarged ventral scutes, more than five dorsal head shields, the eye surrounded by several scales, and the tail long and tapered.

The dorsum is dull dark red, and the venter is paler red. About 50 black rings, equal in width to the red interspaces, are on the body; one or two rings are on the tail. The black rings usually are complete across the venter. Some black rings are irregular, bifurcate laterally, or interconnected middorsally. ♂ 650+21 mm; ♀ 964+23 mm.

Occurrence.—One individual was found on the ground in a clearing at night. Four were obtained during clearing of primary forest by bulldozers; presumably, the snakes were in leaf litter or in the soil.

Life History.—One female collected in June contained small ovarian eggs.



FIG. 136.—*Boa constrictor constrictor*, Santa Cecilia (Photo by Terry D. Schwaner).

BOIDAE

Boa constrictor constrictor Linnaeus

(FIGURE 136)

Material.—Santa Cecilia, 3.

Identification.—This heavy-bodied boid does not have a conspicuously laterally compressed body. All scales on the top of the head and side of the snout (loreal region) are small; there are two rows of large scales between the tip and the orbit. Labial pits are absent. With the exception of *Boa* and *Eunectes*, all other boids in the area have labial pits; of these, *Corallus caninus* and *enydris* have laterally compressed bodies, and *Epicrates cenchria* has a round body. *Eunectes murinus* differs from *Boa constrictor* by having enlarged scales on the anterior part of the head – paired internasals, prefrontals, supraoculars, loreals, and preoculars. Also, the top of the head is dark brown with a pale, broad, diagonal postorbital stripe.

The top of the head is tan with a dark brown middorsal, stripe extending from the snout onto the neck. A broad, dark brown mark extends from the lip nearly to the nostril and posteriorly to the eye; a narrow, vertical, brown bar is present below the eye, and a dark brown postorbital stripe is confluent with the first transverse dark mark on the body. The body is tan or grayish tan anteriorly with rich brown transverse markings de-

limiting ovoid tan blotches; rounded elliptical brown blotches laterally enclose small cream spots. On the posterior third of the body, the dark blotches are reddish brown outlined with dark brown; the tan areas change to cream and are much narrower than those anteriorly. The belly is cream with irregular brown or black flecks and spots anteriorly, and large reddish brown blotches posteriorly. All of our specimens are juveniles, the largest having a body length of 876 mm and a tail length of 98 mm; we have seen individuals in excess of 2 m from the area.

Occurrence.—Boas are uncommon at Santa Cecilia; the three juveniles were found on the airstrip – one in late afternoon and two at night. None was observed during clearing operations at Lago Agrio.

Life History.—We have no reproductive data for this viviparous species from Santa Cecilia. The smallest juvenile (body length 538 mm) was found in November.

Corallus caninus (Linnaeus)

(FIGURE 137)

Material.—Lago Agrio, 1; Santa Cecilia, 7.

Identification.—*Corallus caninus* is one of two arboreal boids in the area which have laterally compressed bodies. Adults are green with white markings, whereas juveniles are reddish brown to yellow with white markings. On the top of the head, the paired internasals are followed by small scales. There are four loreals, two or three preoculars, and deep pits in all of the upper and lower labials. The dorsal scales are smooth and in about 70 rows at midbody. The other arboreal boid is *Corallus enydris*, which has two loreals, one preocular, and pits present only in posterior labials; the dorsum is brown or gray, usually with distinct dark brown or black saddles outlined with cream. Other boids in the area do not have strongly compressed bodies.



FIG. 137.—*Corallus caninus*, ♀, 952 mm SVL (KU 121833).

Adults (body length of 570 mm or more) are dark green above with white markings that usually consist of a mid-dorsal stripe, short transverse bars extending laterally from the middorsal stripe, and short white bars laterally; the ventral surfaces are bright yellow. Two small individuals (440 and 487 mm) are orange-tan and cinnamon-brown dorsally with white markings. Two others (477 and 540 mm) are pale yellow dorsally. ♂ 905+170 mm; ♀ 104+190 mm.

Occurrence.—Most specimens were found by local residents, but I found a juvenile coiled on a limb in second growth forest and an adult coiled on the ground in direct sunlight on the airstrip. Despite these limited observations to the contrary, *Corallus caninus* is known to be primarily nocturnal and arboreal.

Life History.—No reproductive data are available for this viviparous species. The three smallest juveniles (< 500 mm) were found in June, July, and August.

Remarks.—The striking ontogenetic change in color from reddish brown to yellow and green has not been studied.

Corallus enydris enydris (Linnaeus)

Material.—Santa Cecilia, 1.

Identification.—*Corallus enydris* is the least conspicuous of the arboreal boids having laterally compressed bodies. Adults are brown or gray, usually with distinct dark brown or black saddles outlined with cream. On the top of the head, small scales lie posterior to the paired internasals. There are two loreals, one preocular, and deep pits in the posterior upper and lower labials. The dorsal scales are smooth and in about 45 rows at midbody. The other arboreal boid, *Corallus caninus*, has four loreals, two or three preoculars, pits in all labials, and about 70 rows of dorsal scales at midbody; the dorsum is green (reddish brown to yellow in juveniles) with white markings. Other boids in the area do not have strongly compressed bodies.

The single specimen from Santa Cecilia is a male having a body length of 997 mm and a tail length of 247 mm. It is peculiar in having pale coloration and no conspicuous pattern. The dorsum is pale greenish tan with faint salmon blotches and dark brown X-shaped markings with cream borders. The venter is cream with pale brown and salmon markings. The iris is pale green.

Occurrence.—The only individual was found at night on a branch 3.5 m above the ground in secondary forest.

Life History.—No data are available on this viviparous species.

Remarks.—The pale coloration of the specimen resembles that of *Corallus annulatus* (Cope) but the scutellation differs from that species and is like typical *C. enydris* from other localities in Amazonian Ecuador.

Epicrates cenchria cenchria Linnaeus

Material.—Lago Agrio, 1; Santa Cecilia, 8.

Identification.—This round-bodied boa has a distinctive coloration, consisting of three longitudinal dark stripes on the top of the head – one middorsal from

snout to occiput, and paired dorsolateral stripes beginning above the eyes and extending onto the neck, where they may or may not be confluent with the border of the first middorsal spot. A lateral brown stripe extends from the snout, through the eye, to the angle of the jaw. The scales on the top of the head are small except for a pair of enlarged internasals. Pits are present in the lower and anterior upper labials, and the upper labials enter the orbit. The dorsal scales are smooth and in 49 rows at midbody. Other boids in the area have one or two rows of scales separating the labials from the orbit. The two species of *Corallus* have laterally compressed bodies, and *Boa* and *Eunectes* lack labial pits. No other snake in the area has three longitudinal dark stripes on the top of the head and blotches on the body.

The dorsum is brown to reddish brown changing to pale gray or tan laterally; round middorsal orange-tan spots are enclosed with black. Large, round, black, lateral spots enclose cream crescent-shaped marks. The venter is creamy white, and the iris is grayish tan. Characteristically, *Epicrates cenchria* has a blue iridescence in sunlight. ♂ 1650+205 mm; ♀ 1705+215 mm.

Occurrence.—Two were in primary forest, four in secondary forest, and one in a forest-edge situation. Three were active on the ground by day and one at night; one was crawling in a bush and one in a tree at night, and one was coiled in a tree, 5 m above the ground at night. These limited observations suggest that *Epicrates cenchria* probably is nocturnal and terrestrial.

Life History.—No data are available on this viviparous species.

Food.—A juvenile 620 mm in body length contained the remains of a rodent.

Remarks.—Our collections contain only three adults; the other six specimens are juveniles having body lengths of 457–670 mm.

Eunectes murinus murinus (Linnaeus)

Material.—None.

Identification.—This large boid has narrow ventrals and small, smooth dorsals. There are two rows of scales between the labials and the orbit. The scales on the anterior part of the head are differentiated into plates: paired internasals, prefrontals, supraoculars, preoculars, and loreals. Pits are absent in the labials. All other boids in the area have broad ventrals and no more than one row of scales between the labials and the orbit.

The top of the head is dark brown with a pale orange-tan diagonal bar, bordered below by a narrow brown bar, from the eye to the posterolateral corner of the head. The dorsum is gray to grayish tan, with or without a dull greenish tint, and with alternating pairs of dark brown to black, round spots; laterally there are two or three rows of small cream spots, narrowly outlined with black. The belly is dirty creamy white with irregular black marks. This giant snake, the anaconda, attains a length of 11.4 m (Pope, 1961).

Occurrence.—Charles M. Fugler and Ildefonso Muñoz B. (pers. com.) observed individuals in the backwaters of the Río Aguarico behind the island at Santa Cecilia. Ronn Altig obtained one there on 16 February 1974; it had a total length of 2050 mm. Cofan Indians occasionally find the snakes along the same river. I have heard no reports of the anaconda occurring in the lakes or swamps.

Life History.—No data are available on reproduction of this viviparous species in the upper Amazon Basin; Pope (1961) summarized existing data from throughout the range of the species.

COLUBRIDAE

Atractus elaps (Günther)

(PLATE 4)

Material.—Lago Agrio, 4; Santa Cecilia, 23.

Identification.—This predominately red and black snake is highly variable in color pattern and is easily confused with several other snakes having coral snake patterns. The presence of complete rings around the body, or at least across the venter, distinguishes *Atractus elaps* from *Oxyrhopus melanogenys* and *O. petola*, both of which have 19 rows of dorsal scales (15 in *A. elaps*). *Anilius scytale* differs by having the eye beneath a single scale, only five enlarged dorsal head shields, and ventral scutes only slightly wider than the dorsal scales, whereas *Atractus elaps* has the eye surrounded by several scales, seven enlarged dorsal head shields, and enlarged ventral scutes. *Atractus elaps* has a loreal; this scale is absent in most *Micrurus*, but present in *Erythrolamprus aesculapii*, which has a color pattern almost identical to that of some *Atractus elaps*. However, some consistent differences in scutellation serve to distinguish the two species: *A. elaps* has a single anal plate, one pair of chinshields, and one postocular; *E. aesculapii* has a divided anal plate, two pairs of chinshields, and two postoculars.

The dorsal coloration usually consists of red and black rings; the latter normally are somewhat narrower than the red rings, which vary from 8 to 13 ($\bar{x}=11.6$, $N=26$) on the body. Scales in the red areas are tipped with black; in some individuals the black pigment is so extensive as to nearly obliterate the red. Two individuals have red rings about ten times as wide as the narrow black rings, and three have black rings arranged in triads separated by narrow yellow rings, thus having a pattern of red-black-yellow-black-yellow-black-red. The red areas vary from orange-red to vermilion and dark red; usually the color is more intense ventrally. Yellow bars border the black rings ventrally. Usually a narrow yellow or cream transverse line is present on the anterior edges of the prefrontals; in some individuals an incomplete cream or yellow transverse bar is present on the

posterior part of the head, which otherwise is black. ♂ 470+70 mm; ♀ 572+54 mm.

Occurrence.—All individuals were found by day; two were moving in clearings; one was coiled in a building, one was under a log in mature forest, and the others were moving on the ground and amidst leaf litter in mature forest.

Life History.—Two females having body lengths of 506 and 572 mm collected in May each contained six oviducal eggs 29 mm in length. Eight females from May, June, and July contained small ovarian eggs, and two females from April and July showed no evidence of reproductive activity. The smallest juveniles (body lengths of 167 and 182 mm) were found in May and June.

Food.—One individual with a body length of 572 mm contained the remains of a giant earthworm.

Remarks.—Notable sexual dimorphism occurs in the numbers of ventrals and subcaudals: ventrals in males 140-152 ($\bar{x}=146.6$, $N=13$), in females 150-162 ($\bar{x}=154.4$, $N=13$); subcaudals in males 29-34 ($\bar{x}=31.3$, $N=13$), in females 19-24 ($\bar{x}=22.6$, $N=10$). Other features of scutellation are constant: upper labials 6, lower labials 7, loreal 1, postocular 1. The amount of black pigment on scales in the red areas is not correlated with size. Some small individuals have more black pigment than do some large ones. Two specimens (KU 126066-07) have narrow black rings and very wide red rings, but in scutellation these specimens are like the normally patterned specimens.

The ventral surface of the tail of *Atractus elaps* is red with one black bar. Two individuals were observed to elevate and coil the tail so that the bright ventral surface was visible from above. The presumably aposematic tail-coiling behavior is common in many species of snakes having red ventral caudal surfaces (see Myers, 1965, for further discussion).



FIG. 138.—*Atractus major*, ♀, 347 mm SVL (KU 125987).

Atractus major Boulenger

(FIGURE 138)

Material.—Lago Agrio, 11; Santa Cecilia, 14.

Identification.—*Atractus major* is a predominantly brown snake with darker brown dorsal blotches. All other snakes in the area having a similar color pattern have dorsal scales in other than 17 rows, keeled scales, or the vertebral scale row enlarged, except *Liophis cobella*. The latter has straight-edged large, dorsal blotches that usually extend across the venter and a single anal plate. *Atractus major* has irregular dorsal blotches that do not extend onto the ventrals, and a divided anal plate.

The top of the head is brown, dull gray, or black. In juveniles (body length to 180 mm) the posterior part of the head is grayish white; in some larger individuals (body length to 307 mm) the area is dull red, whereas in larger specimens it is brown. A dark brown or black nape band is present. The dorsal ground color varies from tan to brown, sepia, or reddish brown, with or without scattered black flecks. The dorsal blotches are brown to rust, usually outlined with cream, and highly variable in number and shape (Fig. 139). There are 21-52 ($\bar{x}=31.4$, $N=21$) blotches on the body;

the blotches are 1-5 ($\bar{x}=2.8$, $N=21$) scales in length. In most specimens the venter is cream or pale yellow with scattered brown or black flecks, usually concentrated in two medial rows anteriorly and lateral rows posteriorly, but in some individuals of all sizes the venter is predominately brown or dull gray. The tongue is gray with a white tip. ♂ 442+91 mm; ♀ 650+73 mm.

Occurrence.—All individuals were active by day on the ground or in leaf litter, except one, which was concealed beneath a palm frond. One was found in secondary forest, and two were in clearings; all others were in primary forest.

Life History.—Immature ovarian eggs were present in three females collected in May and one in June. A female with a body length of 650 mm contained 12 eggs. The smallest juveniles have body lengths of 145, 150, and 157 mm and are from May, March, and June, respectively.

Food.—One female having a body length of 542 mm contained a giant earthworm.

Remarks.—Notable sexual dimorphism occurs in the numbers of ventrals and subcaudals: ventrals in males 156-168 ($\bar{x}=161.3$, $N=9$), in females 163-180 ($\bar{x}=172.0$, $N=13$); subcaudals in males 41-45 ($\bar{x}=43.1$, $N=9$), in females 27-36

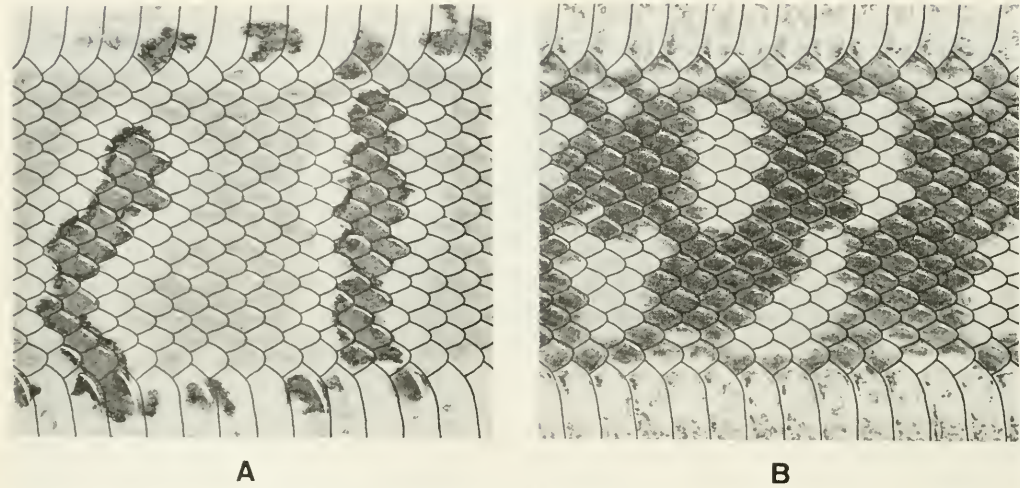


FIG. 139.—Dorsal color pattern at midbody of *Atractus major*. A. KU 125991, B. KU 125998.

($\bar{x}$ =31.1, N =14). Seven upper and seven lower labials occur in all specimens, except one male having eight upper labials on one side and one male having eight lower labials on each side.

Atractus occipitoalbus (Jan)

(FIGURE 140)

Material.—Lago Agrio, 7; Puerto Libre, 8; Santa Cecilia, 2.

Identification.—This small snake with 15 rows of smooth dorsal scales is polymorphic in coloration. Most individuals are dark gray above and below except for a pale chin and occipital collar. Others are brown above with a row of pale spots laterally and a pale belly with a

midventral row of dark spots, fused into an irregular stripe in some specimens. The gray individuals superficially resemble *Ninia hudsoni*, which has keeled dorsal scales in 21 rows. Two other small snakes with smooth dorsal scales are similar to the brown phase of *Atractus occipitomaculatus*, which lacks a preocular and has a long, narrow loreal. *Tantilla melanocephala* lacks a loreal and has a preocular and a divided anal; *Rhadinaca brevirostris* has a loreal, preocular, divided anal, and dorsal scales in 17 rows at midbody, reducing to 15 rows posteriorly. Both *Tantilla* and *Rhadinaca* have longitudinal dark stripes dorsally, and neither has a midventral row of dark spots.

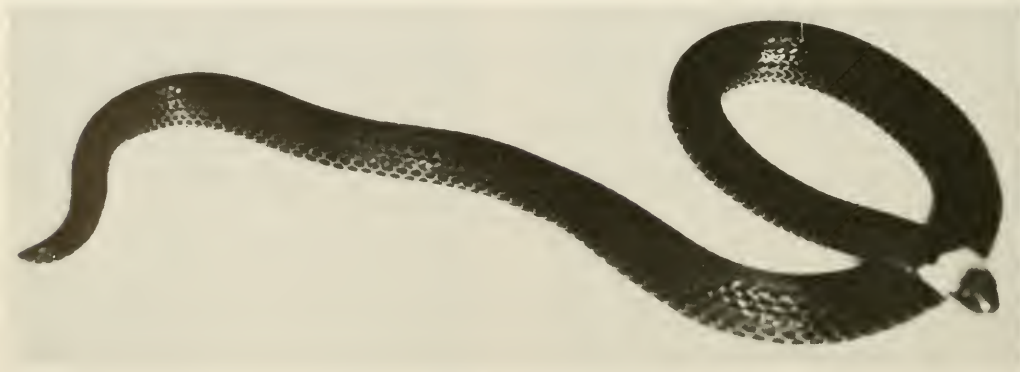


FIG. 140.—*Atractus occipitoalbus*, ♂, 174 mm SVL (KU 121847).

The dark color morphs are dark gray to black above and below; the chin is cream or white, and the occipital collar is dull orange to pinkish orange. The brown morph is grayish brown above with salmon pink spots on the fourth and fifth rows of dorsal scales; the belly is pale yellow, changing to pale orange posteriorly in males, with dark brown spots. ♂ 211+30 mm; ♀ 221+15 mm.

Occurrence.—Three individuals were found under stones at the edge of the forest; five were on the ground in secondary forest, and the others were in primary forest. All were found by day, either moving on the ground or amidst leaf litter, or under rocks and logs. None was in sunlight.

Life History.—One female from May having a body length of 219 mm contained three oviducal eggs 23 mm in length. One female each from March, April, and July contained small ovarian eggs. The smallest juveniles, having body lengths of 69, 80, 85 mm, were found in July, May, and June, respectively.

Food.—One individual contained an earthworm.

Taxonomic Comments.—The range of variation in numbers of ventrals and subcaudals of the brown morph (5 specimens) is encompassed within the range of the more common dark morph (12); ventrals in males 130-137 ($\bar{x}$ =132.8, N =7), in females 142-150 ($\bar{x}$ =145.8, N =10); subcaudals in males 21-26 ($\bar{x}$ =23.3, N =7), in females 12-18 ($\bar{x}$ =14.4, N =10).

Savage (1955) named a striped specimen from Loreto, Ecuador, as *Atractus orcesi*; in the same paper he referred a specimen with pale lateral spots from Sucúa, Ecuador, to *Atractus duboisi* Boulenger. The brown morph from the Santa Cecilia area is the same as the specimen called *Atractus duboisi* by Savage. Savage (1960) placed both of these names of the synonymy of *Atractus occipitoalbus*.

Chironius carinatus (Linnaeus)

(FIGURE 141)

Material.—Santa Cecilia, 10.

Identification.—The presence of dorsal scales in 12 rows on the anterior half of the body distinguishes *Chironius carinatus* from all other snakes in the area, except *C. multiventris*, which differs by having more ventrals and subcaudals and a proportionately longer tail (Table 8). Moreover, the two species exhibit slight differences in adult coloration. In *C. carinatus* the dorsum is greenish olive anteriorly and olive-brown posteriorly, and the upper labials are yellow; in *C. multiventris* the dorsum is dark olive-brown, and the upper labials are tan. The other two species of *Chironius* in the area have dorsal scales in 10 rows and single anal plates; the anal plate in *C. carinatus* is divided.

Adults are dull greenish olive anteriorly and dull olive-brown posteriorly; the belly and upper labials are yellow. The iris is grayish brown, and the tongue is salmon-red with a gray tip. Juveniles are more brightly colored. The dorsum is olive-green anteriorly with a bluish tint laterally and olive-brown posteriorly. The lips, chin, throat, and anterior one-sixth of the body are bright yellow; the rest of the venter is greenish yellow. ♂ 681+384 mm; ♀ 745+405 mm.

Occurrence.—All were sleeping at night. Two were on bushes, and one was 4 m up in a tree in secondary forest; one was 3 m above the ground in a tree and five were in bushes at the edge of the forest.

Life History.—No data are available on reproduction. Eight juveniles were found in April and May.

Food.—An analysis of stomach contents indicates that juveniles eat hylid frogs — adults of *Hyla bifurca*, *garbei*, *punctata*, and *rubra*. One contained three metamorphosing young of *Hyla marmorata*, and another contained two metamorphosing young of an unidentified *Hyla*. *Chironius carinatus* never

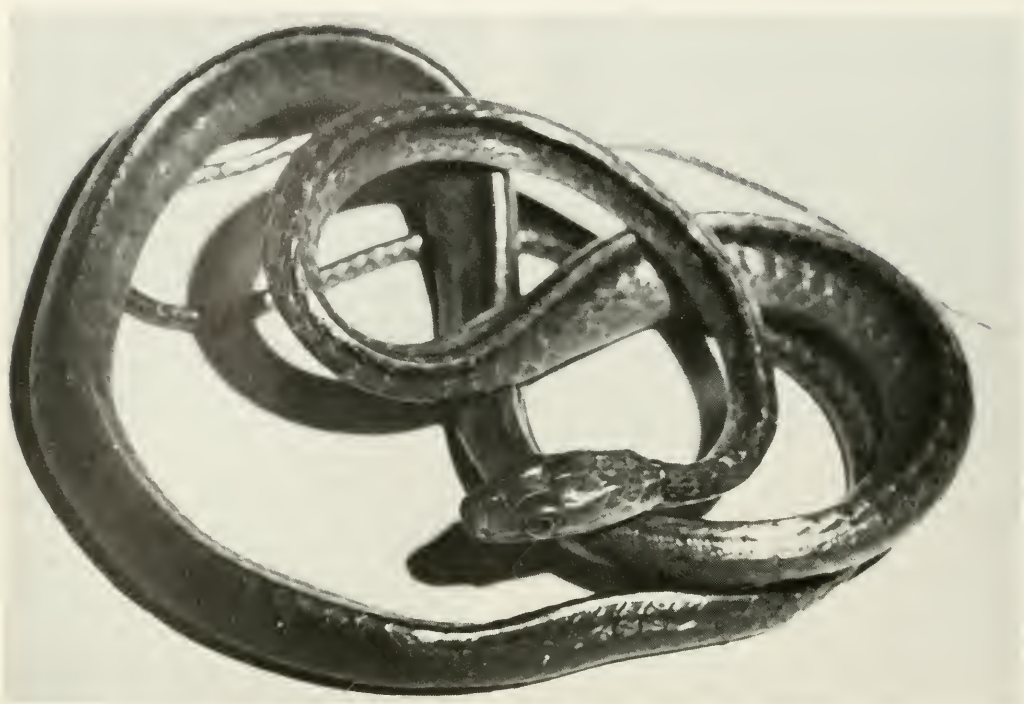


FIG. 141.—*Chironius carinatus*, ♀, 1100 mm SVL; Limoncocha, Provincia Napo, Ecuador (KU 107038).

has been found active at night; thus, it probably finds these nocturnal frogs while they are hidden in dense vegetation by day.

Chironius fuscus (Linnaeus)

(FIGURE 142)

Material.—Puerto Libre, 2; Santa Cecilia, 12.

Identification.—This is one of two snakes in the area having dorsal scales in 10 rows and a single anal plate. The other is *Chironius scurrulus*, which differs from *C. fuscus* by having more ventrals, fewer subcaudals and a proportionately shorter tail (Table 8). The paravertebral scale rows are smooth in *C. scurrulus* and weakly keeled in adult *C. fuscus*. Both juveniles and adults of the two species differ in coloration. Juveniles of *C. scurrulus* are green with rusty orange blotches in larger individuals, and adults are black above and rust

below. Juveniles of *C. fuscus* are tan or gray with brown blotches; adults are brown above and yellow below. The other two species of *Chironius* in the area have 12 rows of dorsal scales.

Considerable ontogenetic change in coloration obtains in *Chironius fuscus*. The smallest juveniles (225 mm) have black-edged brown bands three scales long on the dorsum, separated by gray bands one scale long; the top of the head is olive-brown. With increased size the bands become faint and finally disappear at a body length of 350-400 mm. In small juveniles, the chin and throat are white, becoming progressively darker posteriorly until deep gray on the underside of the tail. In larger individuals the chin and throat are yellow, and the belly is tan; in large adults the chin and throat are bright yellow, and the belly is creamy yellow. The iris varies from gray to brown, usually palest dorsally. ♂ 826+448 mm; ♀ 758+399 mm.

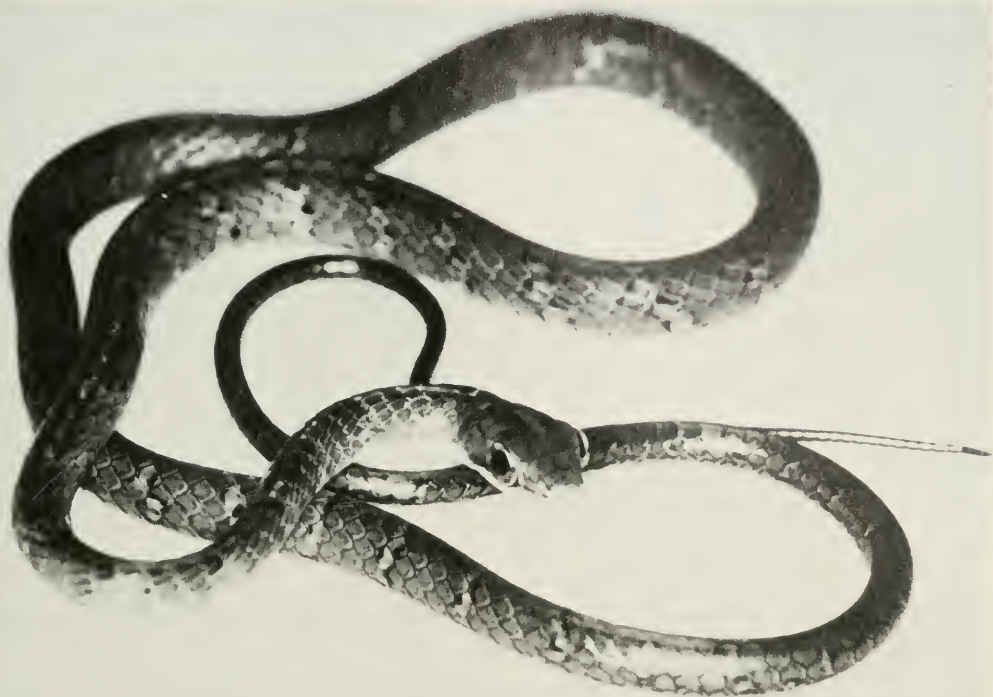


FIG. 142.—*Chironius fuscus*, juvenile, 654 mm SVL (KU 121856).

Occurrence.—Ecological data are available on 11 of 14 specimens. All were sleeping at night on bushes and low trees – seven at heights of less than 1.5 m, and four higher, to 4 m. Seven were in secondary forest and two each in primary forest and at the forest edge. Usually the snakes were loosely coiled on the top of a bush or on a tangle of vines at night. At the slightest disturbance of the bush, the snake dropped to the ground and rapidly crawled away. On two such occasions, snakes were observed to ascend nearby bushes and again assume the sleeping posture.

Life History.—No data are available.

Remarks.—Despite observations on 34 individuals of the four species of *Chironius*, no ecological differences are apparent. All *C. multiventris* were on the ground by day. All *C. carinatus* and *C. fuscus*, and half of the *C. scurrulus* were sleeping on bushes or trees at night. Only one *Chironius (scurrulus)* was ac-

tive in a tree by day. All individuals of *C. carinatus* and *C. fuscus* were associated with forest; 25 percent of the *C. multiventris* and 57 percent of the *C. scurrulus* were found in clearings.

Chironius multiventris
Schnidt and Walker

(FIGURE 143)

Material.—Lago Agrio, 3; Santa Cecilia, 2.

Identification.—This is one of two species of snakes in the area having dorsal scales in 12 rows and a divided anal plate. The other is *Chironius carinatus*, which differs from *C. multiventris* by having fewer ventrals and subcaudals and a proportionately shorter tail (Table 8). Furthermore, adults of the two species differ in coloration. In *C. multiventris*, the dorsum is dark olive-brown, and the upper labials are tan; in *C. carinatus* the dorsum is olive-green anteriorly and



FIG. 143.—*Chironius multiventris*, ♂, 2570 mm SVL (KU 121855).

olive-brown posteriorly, and the upper labials are yellow. The other two species of *Chironius* in the area have 10 rows of dorsal scales.

Adults are dark olive-brown above; the upper labials and side of the head anterior to the eye are olive-tan. The venter is bright yellow. The iris is dark brown, and the tongue is pink with a gray tip. Juveniles are more olive than brown and also have tan labials and yellow venters. ♂ 1660+910 mm; ♀ 1420+840 mm.

Occurrence.—All individuals were found on the ground by day. One was in a clearing and three in primary forest.

Life History.—No data are available.

Taxonomic Comments.—As noted by Schmidt and Walker (1943a:282), *Chironius multiventris* differs from *C. carinatus* principally by having more ventrals and subcaudals; their two specimens from southern Perú had 183 and 178 ventrals and 172 and 202 subcaudals. Peters

and Orejas-Miranda (1970:61) noted that the species was also known from Surinam and Benjamin Constant in western Brasil. In addition to the specimens listed above, there are in The University of Kansas collections specimens from Limoncocha, Provincia Napo, Ecuador, and Belém, Estado do Pará, Brasil.

Chironius scurrulus (Wagler)
(FIGURE 144)

Material.—Santa Cecilia, 12.

Identification.—The presence of dorsal scales in 10 rows anteriorly on the body and a single anal plate distinguishes *C. scurrulus* from all other snakes in the area except *C. fuscus*. The latter differs by having fewer ventrals, more subcaudals, a proportionately longer tail, and faint keels on the paravertebral scale rows in adults (Table 8); all dorsal scales are smooth in *C. scurrulus*. Furthermore, the two species differ in coloration. Juveniles of *C. scurrulus* are green with rusty orange blotches in larger individuals, and adults are black above and rust below. Juveniles of *C. fuscus* are tan or gray with brown blotches; adults are brown above and yellow below. Other species of *Chironius* in the area have 12 rows of dorsal scales.

The smallest specimen (336 mm) is uniform emerald green above and paler green below. In half-grown individuals (600-700 mm) the dorsum is avocado green, slightly darker middorsally; the top of the head is dull brown, becoming green on the temporals and parietals. The chin is white; the rostral, edges of

TABLE 8.—Comparison of Scutellation and Proportions in Four Species of *Chironius* in Amazonian Ecuador.

CHARACTER	<i>C. carinatus</i>	<i>C. fuscus</i>	<i>C. multiventris</i>	<i>C. scurrulus</i>
N	14	15	6	13
Dorsal Scale Rows	12	10	12	10
Keeled Paravertebral Rows	X	X	X	—
Anal Plate	2	1	2	1
Ventrals	137-152	145-154	180-188	153-163
Subcaudals	114-137	118-131	180-197	107-117
Ventrals + Subcaudals	266-281	269-281	362-377	267-279
Tail/Body	0.509-0.608	0.495-0.616	0.548-0.650	0.422-0.522



FIG. 144.—*Chrionius scurrulus*, ♂, 889 mm SVL (KU 121850).

labials and chinshields, and anterior part of belly are rusty orange. Rusty spots are present on various scales throughout the length of the body, especially laterally. In large adults the dorsum is black, and the venter is rust; the edges of the labials are orange. The iris changes from bronze in juveniles to gray to black in adults. ♂ 1575+757 mm; ♀ 1302+550 mm.

Occurrence.—We have ecological data on only seven of the 12 specimens. Four were in clearings and one each was in primary forest, secondary forest, and at the forest edge. By day, one was moving on the ground in primary forest; one was eating a frog in a clearing, and one was found 3 m high in a small tree in a clearing. All others were sleeping on bushes at night.

Life History.—No data are available.

Food.—Four individuals contained frogs: *Leptodactylus mystaceus*, *L. wagneri*, *Hyla lanciformis*, and *H. rubra*. The *Hyla lanciformis* was being eaten by day, when the snake was found amidst a pile of palm fronds in a clearing.

Remarks.—Peters and Orejas-Miranda (1970) did not record this species from Ecuador. In addition to Santa Cecilia, there is one specimen in The Uni-

versity of Kansas collections from Misión Bomboiza, Gualaquiza, Provincia Morona-Santiago, Ecuador, 840 m.

Clelia clelia clelia (Daudin)

Material.—Santa Cecilia, 8.

Identification.—This large snake with smooth scales in 19 rows at midbody (17 posteriorly) undergoes an extraordinary ontogenetic change in coloration. Juveniles (head-body length 600 m) have a black snout and black or dark brown head with a yellow band on the neck and posterior part of the head, followed posteriorly by a wider black band. The rest of the dorsum is red. In the smallest juveniles the dorsum is bright red; in larger ones the red is duller and the tips of the scales, especially mid-dorsally, are dark brown or black. Individuals 600-900 mm in head-body length are dull reddish brown to brownish black; in these the yellow nape band becomes suffused with brown and then black. In large adults the entire dorsum is black. The dorsal color extends onto the edges of the ventrals and subcaudals, both of which are immaculate cream throughout development; the chin, lower

labials and ventral parts of the upper labials also are cream.

Juveniles are easily confused with *Drepanoides anomalus*, *Pseudoboa coronata*, and *Oxyrhopus formosus*. *Drepanoides* has 15 rows of dorsal scales, and *Pseudoboa* has 17 rows; in both of these, only the snout is black, and the head from the eyes posteriorly onto the neck is creamy yellow. In *Oxyrhopus formosus* the tip of the snout is white; in adults, which are colored like *Clelia*, the top of the head and nape are brown or black, whereas in juveniles, which have bands on the body, the top of the head is brown or black, and the nape is cream. Furthermore, *Oxyrhopus formosus* has fewer than 215 ventrals; *Clelia* has more than 215. Adults of *Clelia clelia* can be confused with the uniform black *Drymoluher dichrous*; the latter species has dorsal scales in 15 rows and a single anal plate, whereas *Clelia* has 19 rows and a divided anal plate.

The middorsal scale row in *Clelia* is slightly enlarged. Variation in scutellation is given in Table 9 (see accounts of *Oxyrhopus*). The iris is reddish brown. ♂ 1057+157+ mm (incomplete); ♀ 2070+280+ mm (incomplete).

Occurrence.—Four specimens lack ecological data. One was moving on the ground in a clearing in the early morn-

ing. One was in water in an open marsh at night, and two were moving on the ground at night in a clearing. These limited data suggest that the species may be primarily nocturnal and definitely terrestrial.

Life History.—A female collected in May, and 2070 mm in body length, contained 20 immature ovarian eggs.

Food.—One individual had eaten a diurnal snake, *Leimadophis reginae*. Another contained an unidentified rodent and when found at night was eating an *Ameiva ameiva*, which evidently had been discovered in a nocturnal retreat.

Dendrophidion dendrophis (Schlegel)

Material.—Santa Cecilia, 2.

Identification.—Only two snakes in the area have keeled dorsal scales in 17 rows at midbody. *Dendrophidion dendrophis* and *Drymobius rhombifer*. In the latter the anal plate is divided, whereas in *Dendrophidion* it is single. Both species have dark brown or black dorsal blotches; in *Dendrophidion* the blotches have straight, transverse edges and extend laterally to the first scale row, whereas in *Drymobius* the blotches are ovoid, much wider middorsally than laterally, and extend laterally to the second or third scale row. Juveniles of *Drymo-*

TABLE 9.—Scutellation in Species of *Clelia* and *Oxyrhopus* in Amazonian Ecuador.
(Means in parentheses below observed ranges.)

CHARACTER N	<i>C. clelia</i> 3 ♂, 5 ♀	<i>O. formosus</i> 1 ♂, 5 ♀	<i>O. petola</i> 11 ♂, 11 ♀	<i>O. melano-</i> <i>genys</i> 9 ♂, 5 ♀
Preocular in contact with frontal	-----	-----	X	X
Upper Labials	7-8 (7.6)	8	8-9 (8.1)	8-9 (8.1)
Lower Labials	8	8-10 (8.7)	10-11 (10.4)	9-10 (9.9)
Ventrals ♂ ♂	218-225 (221.5)	191	206-221 (214.5)	187-198 (191.9)
..... ♀ ♀	228-242 (234.2)	194-208 (199.2)	209-225 (216.7)	201-206 (204.0)
Subcaudals ♂ ♂	94-96 (95.0)	95	110-122 (116.7)	82-94 (88.0)
..... ♀ ♀	77-86 (82.5)	74-80 (76.4)	99-112 (103.8)	76-84 (78.8)

luber dichrous have a body pattern similar to that of young *Dendrophidion*, but in the latter the head is unicolor brown, whereas in *Drymoluber* the head is tan or gray with dark brown markings. Furthermore, *Drymoluber* has smooth dorsal scales in 15 rows.

The top of the head is olive-brown. The body has 49-55 dark brown blotches 3 scales in width, separated by narrow ($\frac{1}{2}$ scale in width) creamy tan interspaces on the anterior half of the body. The anterior edge of each blotch is dark brown or black posteriorly the pale interspaces do not extend across the body, so the blotches are delimited only by their dark anterior borders. Laterally the interspaces are orange. The dorsal scales on the anterior part of the body have faint blue edges. The chin and throat are white, and the belly is lemon yellow. The tongue is gray. ♀ 670+90+ mm (incomplete).

Occurrence.—Ecological data are available for only one specimen, an adult female which was sleeping at night on a bush in primary forest. My observations on this species in Central American and elsewhere in the Amazon Basin show conclusively that it is an active diurnal, terrestrial species, inhabiting forest.

Life History.—A female from June contained six ova 30.2 mm in length.

Food.—The adult female contained an adult frog, *Eleutherodactylus conspicillatus*.

Taxonomic Comments.—The taxonomic status of Amazonian *Dendrophidion* is unsettled, but the late James A. Peters, who was studying *Dendrophidion*, examined the two specimens from Santa Cecilia and tentatively referred them to *D. dendrophis*.

Remarks.—These snakes have long tails which break readily. Most adults in museum collections have incomplete tails. A juvenile from Santa Cecilia has a body length of 318 mm and a tail length of 246 mm. Assuming approximately the same ratio in the adult, the

adult female from Santa Cecilia must have had a tail length of about 515 mm.

Dipsas catesbyi (Sentzen)

(FIGURE 145)

Material.—Lago Agrio, 2; Puerto Libre, 1; Santa Cecilia, 28.

Identification.—Of the three species of *Dipsas*, the only snakes in the area having dorsal scales in 13 rows and an enlarged vertebral row, this is the only species having a loreal and a preocular. *Dipsas indica* has a preocular and no loreal, and *D. pavonina* has a loreal and no preocular. Furthermore, *D. catesbyi* has only one anterior temporal, whereas the other species of *Dipsas* have two. Other snakes having an enlarged vertebral scale row have the dorsal scales in 15 (*Imantodes lentiferus*), 17 (*Imantodes cenchoa*) or 19 (*Leptodeira* and *Tripanurgos*) rows.

The head is black with a white line across the snout; usually the line continues across the chin. The dorsum is marked by paired elliptical dark brown blotches, meeting or not, middorsally. The dark chocolate brown blotches are bordered with white, especially anteriorly, and stand out in marked contrast with the reddish brown ground color. The venter is white with longitudinal black marks and flecks, especially posteriorly. The iris is reddish brown. ♂ 489+191 mm; ♀ 526+200 mm.

Occurrence.—All active individuals were found at night. Twelve were in primary forest, seven in secondary forest, and one in a banana grove. Individuals most frequently were observed crawling slowly along branches of bushes and trees, some as high as 4 m above the ground. Two were retrieved from the tops of large trees (> 20 m) when the trees were felled by day. One individual was crawling on the forest floor at night.

Life History.—Three females (April 2, June 1) contained 1, 4, 1 oviducal eggs, the largest 35.3 mm in length. The smallest juvenile (193 mm) is from June.



FIG. 145.—*Dipsas catesbyi*, ♀, 514 mm SVL (KU 146736).

Three others have body lengths of 216 mm (March), 224 and 230 mm (July).

Remarks.—By comparison with Peters' (1956) analysis of variation in *Dipsas catesbyi*, our material from Santa Cecilia is rather uniform. There is variation of one or two preoculars and postoculars; in one individual the loreal is fused with the preocular on both sides of the head.

No ecological differences are apparent among the three species of *Dipsas* in the area. I have the general impression that *Dipsas indica* is more commonly found in dense, shrubby vegetation than the other species, but there are too few observations on that species to substantiate the impression. Perhaps the three species feed on different species of snails; *Dipsas indica* has a proportionately larger head and heavier body than the other species and thus possibly feeds on larger snails.

Dipsas indica ecuadorensis Peters

(FIGURE 146)

Material.—Puerto Ore, 1; Puerto Libre, 1; Santa Cecilia, 11.

Identification.—This blunt-headed snake with dorsal scales in 13 rows and the enlarged vetrebral row differs from other species of *Dipsas* by lacking a loreal and having a single preocular. *Dipsas catesbyi* has a loreal and preocular, and *D. pavonina* has a loreal and no preocular; furthermore *D. pavonina* has three postoculars, whereas *D. indica* has two. Moreover, *D. indica* is the only species of *Dipsas* in the area having a dark venter. Other snakes having an enlarged vertebral scale row have the dorsal scales in 15 (*Imantodes lentifer*-



FIG. 146.—*Dipsas indica ecuadorensis*, ♀, 821 mm SVL; Bermejo, Provincia Napo, Ecuador (KU 121871).



FIG. 147.—*Dipsas pavonina*, ♀, 477 mm SVL; Pilcopata, Departamento Cuzco, Perú (KU 139422).

us), 17 (*Imantodes cenchoa*), or 19 (*Leptodeira* and *Tripanurgos*) rows.

The head is brown with pale yellow and dark brown longitudinal streaks; the body is gray or grayish brown with dark brown blotches that are wider ventrally than dorsally. The throat is pale yellow, suffused with gray in some individuals, and small yellow spots are present ventrolaterally. The belly is dark brown. The iris is grayish green. ♂ 510+197 mm; ♀ 732+242 mm.

Occurrence.—All individuals were on branches or leaves of bushes and trees at night. Six were in second growth forest; the others were in primary forest. Two were on vegetation higher than 1.5 m above the ground; the others were on lower vegetation. Three were obtained in July, two each in April, May and August; no more than one was found in any other month.

Life History.—None of the three adult females contained eggs. The smallest juvenile (264 mm) was found in January.

Food.—One individual contained the remains of the body of a snail.

Dipsas pavonina Schlegel

(FIGURE 147)

Material.—Puerto Libre, 1; Santa Cecilia, 2.

Identification.—This slender *Dipsas* with dorsal scales in 13 rows and an enlarged vertebral row differs from the other *Dipsas* in the area by having three postoculars, a loreal, and no preoculars. *Dipsas catesbyi* has a loreal and preocular, and *D. indica* has a preocular and no loreal; both species have two postoculars. Furthermore, *D. pavonina* differs in coloration; the belly is uniformly pale tan, whereas the belly is dark brown in *D. indica* and white with black streaks in *D. catesbyi*. In the latter, the body blotches are elliptical, narrower dorsally and ventrally than laterally, whereas in *D. pavonina* the blotches extend across the body and are wider dorsally than ventrally. Other snakes having an enlarged vertebral scale row have the dorsal scales in 15 (*Imantodes lentiferus*), 17 (*Imantodes cenchoa*), or 19 (*Leptodeira* and *Tripanurgos*) rows.

The head is black with a narrow white line across the snout that extends onto the lower labials but not across the chin. The nape band and first four or five spaces between the black blotches are white. The interspaces become progressively more tan posteriorly, but a narrow white border persists around the blotches. The blotches are much broader than the interspaces, extend across the body to the first row of dorsal scales,

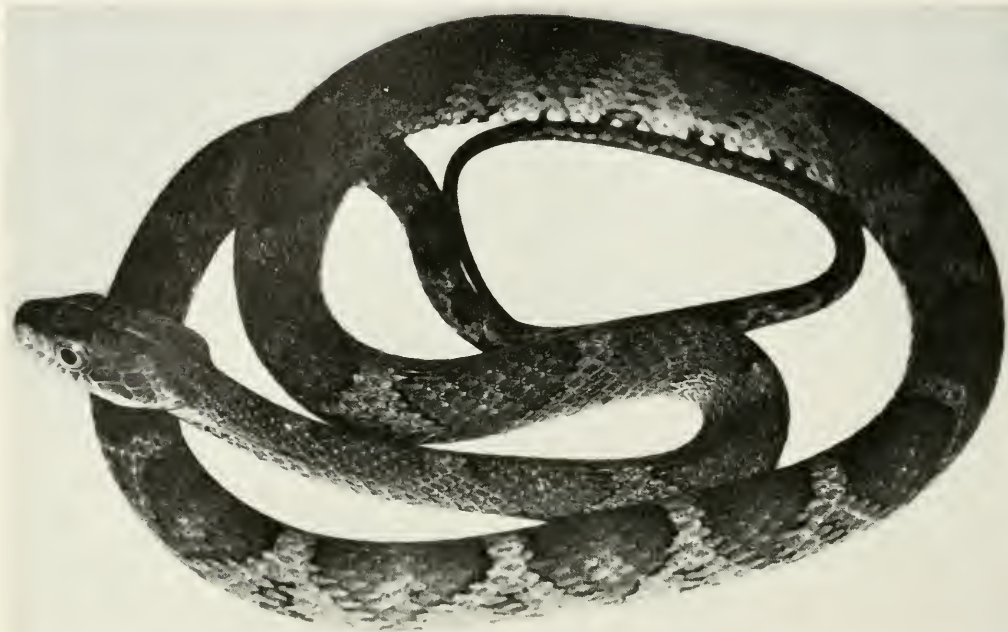


FIG. 148.—*Drymobius rhombifer*, ♀, 1111 mm SVL (KU 121878).

and are slightly wider dorsally than laterally. The venter is uniformly tan. The iris is dull brown. ♂ 446+206 mm; ♀ 381+176 mm.

Occurrence.—All were active at night – two in primary forest and one in secondary forest. One was crawling up a tree trunk about 2 m above the ground; one was crawling along a vine about 3 m above the ground, and the other was on a limb about 1.5 m above the ground.

Life History.—No life history data are available.

Drepanoides anomalus (Jan)

Material.—Durenó, 1.

Identification.—This red snake with a black snout, creamy white head, and black nape band differs from other similarly colored species by having the dorsal scales in 15 rows. *Pseudoboa* has 17 rows, and *Clelia* and *Oxyrhopus* have 19 rows. The snout, including all scales anterior to the eye, the anterior part of the frontal, and the anterior part of the

chin, is black. The rest of the head and nape are creamy white. The nape color is bordered posteriorly by a black band six scales wide. The rest of the dorsum is red with black on the posterior tips of the scales. The dorsal color does not extend onto the cream venter.

The single specimen is a male having 173 ventrals, 78 subcaudals, single anal plate, six upper and lower labials, one preocular, two postoculars, and no loreal. ♂ 330+109 mm.

Occurrence.—One was crawling on the ground in a clearing at night.

Life History.—No data are available.

Drymobius rhombifer (Günther)

(FIGURE 148)

Material.—Puerto Libre, 2; Santa Cecilia, 4.

Identification.—This is one of two snakes in the area having keeled dorsal scales in 17 rows at midbody. The other, *Dendrophidion dendrophis* has a single anal plate and straight-edged, transverse



FIG. 149.—*Drymoluber dichrous*, juvenile, 334 mm SVL (KU 121882).

body blotches extending to the first scale row. *Drymobius rhombifer* has a divided anal plate and ovoid body blotches that are much wider middorsally than laterally and extend laterally to the second or third scale row. The color pattern of juvenile *Drymobius* is similar to that of juveniles of *Xenodon severus* and *Bothrops atrox*. The latter has keeled dorsal scales in 25 rows at midbody and a large pit between the nostril and the eye. *Xenodon* has smooth dorsal scales in 21 oblique rows.

Juveniles are grayish tan with darker blotches, which are chocolate brown peripherally and reddish or grayish brown centrally. The top of the head is olive-tan with dark brown spots on the parietals; the side of the head is grayish white. The chin and throat are pale gray; the rest of the venter is cream with irregular, dark brown marks laterally. The coloration has less contrast in adults. The dorsal ground color is darker, so the blotches are not as distinctive; blotches on the head are indistinct. The venter is grayish white. The iris is bronze. ♂ 907+361 mm.

Occurrence.—Four individuals of this diurnal, terrestrial snake were in primary forest, and two were in secondary forest. Two individuals were sleeping in low bushes at night. Two were taken in July and one each in February, March, April, and May.

Life History.—No data are available.

Food.—One individual contained remains of an unidentifiable lizard.

Drymoluber dichrous (Peters)

(FIGURE 149)

Material.—Puerto Libre, 2; Santa Cecilia, 5.

Identification.—The combination of smooth dorsal scales in 15 rows, no enlarged vertebral scale row, two anterior temporals and a single anal plate distinguishes *Drymoluber* from all other snakes in the area, except *Drepanoides anomalus*, which has a white head, with a black snout and nape band, and a red body. Adult *Clelia clelia* are colored like adult *Drymoluber*, but *Clelia* has 19 rows of dorsal scales and a divided anal plate.

The ontogenetic change in coloration involves a juvenile blotched pattern dorsally that changes to uniform black in adults. In juveniles, the top of the head is pale gray with two transverse brown marks and a pair of large brown parietal spots. The side of the head is grayish white with brown vertical markings. The dorsal ground color is reddish tan with dark reddish brown blotches becoming darker posteriorly. The blotches are 2-3 scales wide, have straight edges, and extend onto the edges of the ventrals. Anteriorly the interspaces are 2-3 scales wide; posteriorly they become progres-

sively narrower until they disappear on the proximal part of the tail. The chin and throat are white with black marks; the rest of the venter is creamy gray. Adults are uniformly black above and cream below. The edges of the ventrals are black, and the upper labials are cream. The iris is tan dorsally with the remainder dark reddish brown, and the tongue is black. ♂ 900+322 mm; ♀ 725+145 mm.

Occurrence.—This diurnal, terrestrial snake sleeps in low vegetation at night. Three individuals were in primary forest and one in secondary forest.

Life History.—No data are available.

Food.—One individual disgorged two lizards — *Neusticurus ecleopus* and *Anolis* (unidentifiable to species).

Erythrolamprus aesculapii aesculapii
(Linnaeus)
(PLATE 4)

Material.—Lago Agrio, 2; Santa Cecilia, 3.

Identification.—Three genera of snakes in the area have dorsal scales in 15 rows and patterns of red, yellow, and black rings. Of these, *Atractus elaps* differs by having a single anal plate and one pair of chinshields. *Erythrolamprus* and the four species of *Micrurus* have divided anal plates and two pairs of chinshields. *Erythrolamprus* differs from *Micrurus* by having two (instead of one) secondary temporals and by lacking a poison fang anteriorly on the maxillary. The coloration of the head of *Erythrolamprus* differs from that of all *Micrurus*, except *M. lemniscatus*. In the latter, the snout is black, and there is a yellow band anterior to the eyes. In *Erythrolamprus* the snout is yellow with a black band enclosing the eyes and a yellow band posterior to the eyes.

The snout is yellow-tan, followed by a broad black band enclosing the eyes, and a broad yellow band extending nearly to the posterior tips of the parietals. The nape is black, interrupted or not, by a narrow yellow ring. The body pattern

of rings (red-black-yellow-black-red) commences posterior to the nape. The black rings are four or five scales wide middorsally and only two or three scales wide ventrally. The yellow rings are two or three scales wide, and the red rings are five or six scales wide. The posterior tips of the scales in the yellow and red rings are black. One individual has the first red ring 27 scales wide; the rest of the pattern is normal. ♂ 534+64 mm; ♀ 667+89 mm.

Occurrence.—All individuals were on the forest floor by day; one was in secondary forest, and the others were in primary forest.

Life History.—Females from May and October contained immature ovarian eggs.

Food.—Two individuals had eaten snakes: *Atractus occipitoalbus*.

Remarks.—When disturbed, one individual elevated the head and spiraled the tail upward. It is questionable why this presumably aposematic behavior was displayed by *Erythrolamprus aesculapii*, because the ventral surface of the tail is red like the dorsum.

***Helicops angulatus* (Linnaeus)**
(FIGURE 150)

Material.—Puerto Libre, 1; Santa Cecilia, 7.

Identification.—The small eyes, dorsal nostrils, and small, single internasals distinguish snakes of the genus *Helicops* from others in the area. *Helicops angulatus* has keeled dorsal scales in 19 rows at midbody (17 rows posteriorly) and one anterior temporal, whereas *Helicops petersi* has 21 rows at midbody (17 rows posteriorly) and two anterior temporals. The two species also differ in color pattern. *Helicops angulatus* has about 20 distinct, dark brown blotches across the dorsum and extending onto, or continuous across, the venter. *Helicops petersi* has about 40 indistinct middorsal dark blotches alternating with smaller lateral blotches.

The dorsal ground color varies from

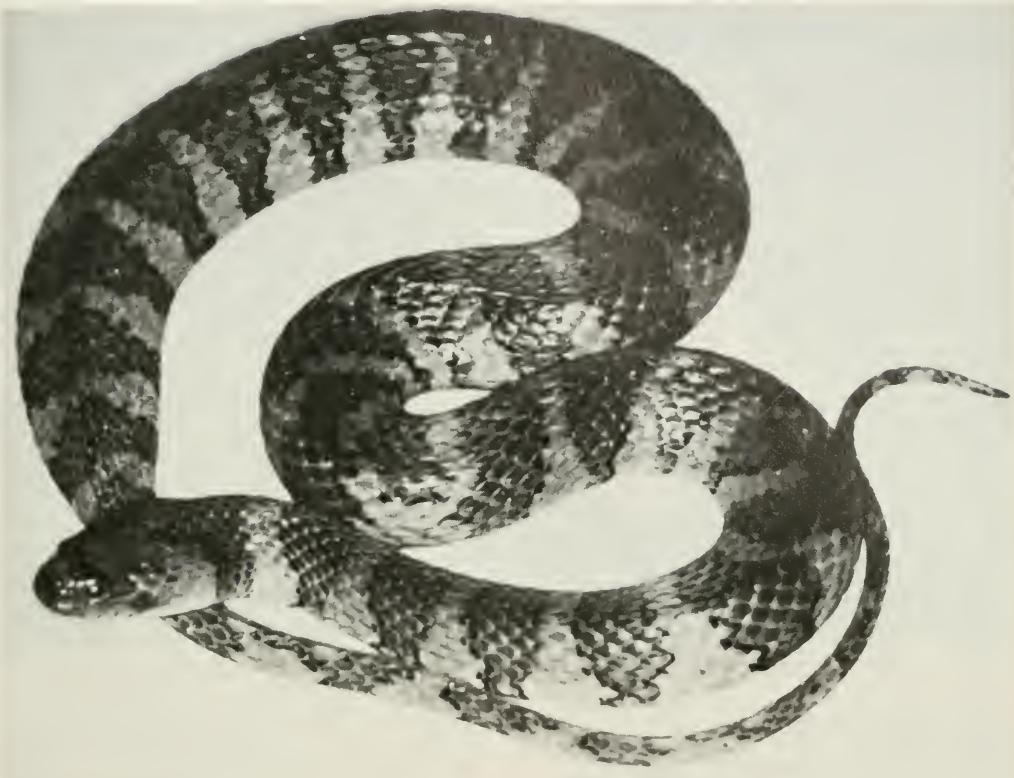


FIG. 150.—*Helicops angulatus*, ♀, 666 mm SVL (KU 121885).

olive-green to dull brown with dark brown blotches that are reddish brown centrally in some individuals and narrowly bordered by black in some specimens. The top of the head is olive-brown with a dark brown interorbital bar evident in some individuals. The chin is white to lemon yellow, and the belly is creamy yellow to orange with dark brown to black extensions of the dorsal blotches. The ventral surface of the tail is banded black and creamy gray in juveniles and dull gray in some adults. The iris is dull olive-brown. ♂ 315+162 mm; ♀ 475+191 mm.

Occurrence.—One individual was at the edge of the river by day. All others were found in water – small pools or streams at night.

Life History.—One female from June having a body length of 475 mm contained 11 ovarian eggs.

Food.—One individual contained the remains of an unidentifiable tadpole.

Remarks.—These snakes depress the body, flatten the neck and bite viciously.

***Helicops petersi* Rossmann**

Helicops petersi Rossmann, 1976, Occas. Pap. Mus. Zool. Louisiana State Univ., 50:2
Type locality.—Mishualli River, 1 mi NE Tena, Provincia Napo, Ecuador[.]

Material.—Puerto Libre, 1; Santa Cecilia, 2.

Identification.—This snake, like *Helicops angulatus*, has small eyes, dorsal nostrils, and a single internasal, thereby differing from all other snakes in the area. *Helicops petersi* has keeled dorsal scales in 21 rows at midbody (17 rows posteriorly) and two anterior temporals, whereas *Helicops angulatus* has 19 rows at midbody (17 rows posteriorly) and one anterior temporal. Furthermore, *H.*

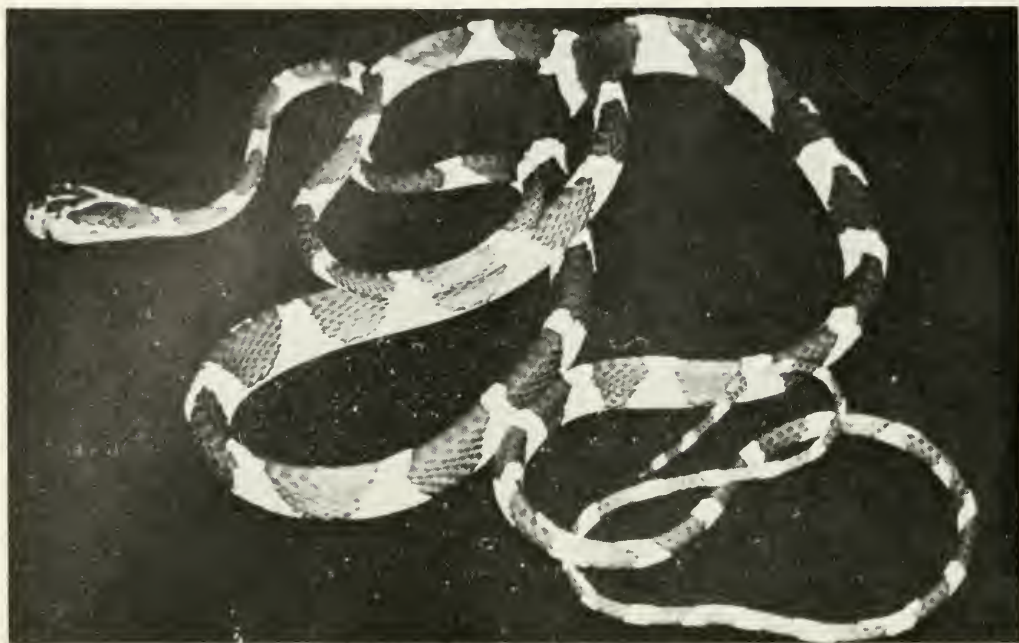


FIG. 151.—*Imantodes cenchoa cenchoa*, juvenile, 551 mm SVL (KU 121890).

petersi differs from *H. angulatus* in coloration; the former has about 40 indistinct middorsal blotches alternating with smaller lateral blotches and a dark venter, whereas the latter has about 20 distinct middorsal blotches extending onto, or across, the pale venter.

The dorsum is dull yellowish tan to grayish tan with olive-brown to dark gray blotches; the venter is gray to black with cream to tan transverse streaks. The iris is tan. ♂ 444+225 mm; ♀ 340+29+mm.

Occurrence.—One individual was partially buried in the sand at the edge of the river by day; the others were in a back water of the river at night.

Life History.—A female collected in July has a body length of 340 mm and contained 12 small ova.

Remarks.—The limited data suggest that *H. petersi* is limited to major rivers, whereas *H. angulatus* is more widespread, inhabiting small streams, swamps, and temporary pools.

Imantodes cenchoa cenchoa (Linnaeus)

(FIGURE 151)

Material.—Lago Agrio, 2; Puerto Libre, 1; Santa Cecilia, 32.

Identification.—This long, slender snake with a small, blunt head and laterally compressed body with a greatly enlarged vertebral scale row has the dorsal scales in 17 rows. No other snake in the area has enlarged vertebral scales and dorsal scales in 17 rows. *Imantodes lentiferus* has 15 rows of scales and smaller reddish tan dorsal blotches, whereas *I. cenchoa* has larger dark brown blotches. Of the other genera having an enlarged vertebral scale row, *Dipsas* has dorsal scales in 13 rows and *Leptodeira* and *Tripanurgos* in 19 rows.

The top of the head is dark brown; the edges of the scales are cream. The transverse body blotches are dark chocolate brown, and the interspaces are cream to tan. The belly is cream to yellowish tan with small brown flecks. The iris is creamy tan, with a greenish tint in some

individuals. ♂ 811+357 mm; ♀ 827+345 mm.

Occurrence.—This nocturnal, arboreal snake is about equally abundant in primary and secondary forest. Two-thirds of the individuals were found at heights of less than 1.5 m above the ground; others were found to heights of 4 m. One individual was coiled in a bamboo stump by day. These snakes are capable of extending more than half their total length into space and require only a flimsy branch on which to rest the chin before proceeding to move from one branch to another.

Life History.—Four of nine (44.4%) of the adult females are gravid. Females with oviducal eggs were found in March, June, July, and November. Three contained two eggs, and one had one egg. The largest egg was 29.6 mm in length. Small juveniles (314-347 mm) were obtained in May (2), June (1), July (1), and August (1). These data support Fitch's (1970:152) contention that *Imantodes cenchoa* breeds throughout the year.

Food.—Two individuals contained lizards — *Anolis fuscoauratus* and *A. punctatus*.

Remarks.—Both *Imantodes cenchoa* and *I. lentiferus* are active primarily in low vegetation at night. The latter has been found only in secondary forest, whereas *I. cenchoa* is equally abundant in primary and secondary forest. With increased human disturbance of the forest at Santa Cecilia, *I. lentiferus* seems to be increasing in abundance relative to *I. cenchoa*. The ratio of specimens of *I. cenchoa* to *I. lentiferus* in collections made in 1968-69 is 4:1, in 1970-71 1:1. The limited data on stomach contents reveals definite differences in food preferences — lizards in *I. cenchoa* and frogs in *I. lentiferus*.

Imantodes lentiferus (Cope)

Material.—Puerto Libre, 3; Santa Cecilia, 24.

Identification.—The presence of a greatly enlarged vertebral scale row, slender laterally compressed body, and small blunt head distinguish this species from all other snakes in the area, except *Imantodes cenchoa*. The latter has 17 rows of dorsal scales, whereas *I. lentiferus* has 15 rows. Furthermore, *I. lentiferus* has smaller reddish tan body blotches, and *I. cenchoa* has larger dark brown blotches. Of the other genera having an enlarged vertebral scale row, *Dipsas* has dorsal scales in 13 rows and *Leptodeira* and *Tripanurgos* in 19 rows.

The top of the head is tan with three dark brown spots, fused into one spot in larger individuals. The body is pale tan with brown to reddish brown blotches, narrowly outlined with dark brown, much narrower laterally than dorsally, and extending laterally to the second or third row of scales. The chin is white or cream; the belly is pinkish tan with small black flecks. The iris is yellowish tan. ♂ 682+308 mm; ♀ 710+291 mm.

Occurrence.—All individuals were found in secondary forest; three-fourths of the individuals were crawling in bushes and herbs at heights of less than 1.5 m above the ground, whereas others were found higher in bushes and trees.

Life History.—One female (667 mm) deposited three eggs (10 mm in diameter and 20, 23, and 25 mm long) on 14 August. Two eggs hatched on 25-26 November. John Simmons (field notes, 25 November 1971) described the hatching: 0820 hr, 22°C, head appeared in slit 5 mm long. 1200 hr, 28°C, head still in slit, now about 7 mm long. 1310 hr, head withdrawn into shell. 1600 hr, head again in slit. 1707 hr, 27°C, second slit on opposite side of shell. 1730 hr, 25.5°C, approximately 25 mm of head and neck extended through second slit and at angle of about 45° from axis of egg; flicking of tongue. 1800 hr, dusk, snake rapidly emerged from shell and crawled onto plants. The hatching of the second egg on 26 November corresponded to the

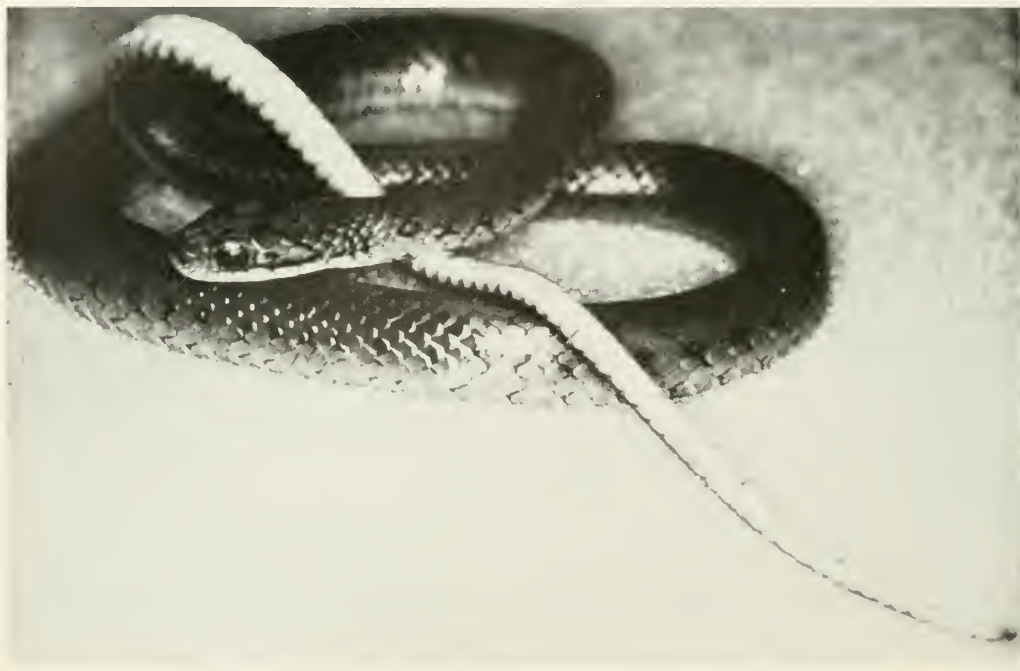


FIG. 152.—*Leimadophis reginae*, ♂, 575 mm SVL (KU 121324).

first. Again, two slits were made. The first was noted at 0740 hr; the snake emerged from the egg near dusk, 1745 hr. Perhaps the time of emergence was purposefully delayed until dusk, at which time these snakes normally become active. The young had body lengths of 197 and 204 mm and tail lengths of 82 and 87 mm. Two slightly larger juveniles (243 mm) were found in July.

Food.—Stomach contents of four individuals consisted only of frogs: *Hyla calcarata*, *Hyla geographica*, *Eleutherodactylus lacrimosus*, and *Eleutherodactylus* sp.

Remarks.—See the account of *Imantodes cenchoa cenchoa* for a discussion of the ecological relationships of the two species of *Imantodes*.

Leimadophis reginae (Linnaeus)

(FIGURE 152)

Material.—Dureno, 4; Lago Agrio, 1; Santa Cecilia, 8.

Identification.—The presence of

smooth dorsal scales in 17 rows at mid-body and a divided anal plate distinguish this species from all others in the area except *Leimadophis* sp., *Rhadinaea brevirostris*, and *Liophis cobella*. The latter has dark bands encircling the body, and *Rhadinaea* has distinct dark brown and tan stripes dorsally and an immaculate venter. Both species of *Leimadophis* have black transverse marks or a checkerboard pattern on the belly and lack distinct dorsal stripes, at least anteriorly. In *Leimadophis reginae* the upper lip is cream, whereas in *L. sp.* the edge of the upper lip is dark, delimiting a white labial stripe. *Leimadophis* sp. has 157 ventrals, and *L. reginae* has fewer than 150 ventrals.

The dorsum is tan with a trace of green anteriorly on the first two scale rows. A narrow dark brown line extends from the nostril through the lower edge of the orbit to the angle of the jaw. A faint dark brown stripe usually is evident posteriorly (beginning about two head lengths anterior to the anus) on the

third scale row and extends to the tip of the tail. The chin and throat are immaculate cream; the belly and underside of the tail are yellow with irregular transverse black bars. The iris is gold above and reddish brown below, and the tongue is dark gray. ♂ 391+145 mm; ♀ 436+127 mm.

Occurrence.—Most were found active on the forest floor by day; one was in secondary forest and the others in primary forest. One was active in a clearing by day. Four were found in August, three in May, two in July, and one each in February, April, and September.

Life History.—One female collected in February contained three oviducal eggs 27.5 mm in length, and one from April contained six maturing ovarian eggs 22.9 mm in length. Fitch (1970:137) noted that "Gravid females of *L. reginae* are represented in the Bassler Collection from Iquitos, Perú, for each month of the year, except for May, July, and October when no adult females were collected, and January and April, each represented by only one adult female."

Food.—One individual contained an adult *Leptodactylus wagneri* and numerous, small tadpoles of *Hyla lanciformis*.

Leimadophis sp.

Material.—Santa Cecilia, 1.

Identification.—This is one of four snakes in the area having smooth dorsal scales in 17 rows at midbody and a divided anal plate. Of these, *Liophis cobella* has dark bands encircling the body, and *Rhadinaea brevirostris* has distinct dark brown and tan stripes dorsally and an immaculate venter. *Leimadophis* sp. and *L. reginae* have transverse black marks or a checkerboard pattern of black marks on a cream venter. In *Leimadophis* sp. the edge of the upper lip is dark, delimiting a white labial stripe, and in *L. reginae* the entire upper lip is cream. *Leimadophis reginae* has fewer than 150 ventrals, whereas *L. sp.* has 157.

The top of the head and middorsum of the body and tail are dark brown; on the body the dark brown fades to tan on scale rows 3-5 and to cream on scale rows 1-2. Posteriorly, the scales on the fourth scale row are edged with dark brown, thereby giving them a darker appearance and an illusion of a tan stripe on the fifth scale row. The upper labials are white with a dark brown lower edge. The lower labials and chin are black and white, and the belly is cream with irregular, black transverse marks. The underside of the tail is immaculate cream. ♂ 250+57+ mm (incomplete).

Occurrence.—The single specimen was dead on a trail in the forest by day.

Life History.—No data are available.

Taxonomic Comments.—Charles W. Myers has studied this specimen (KU 112275) and is unsure if an available name exists.

Leptodeira annulata annulata (Linnaeus)

(FIGURE 153)

Material.—Puerto Ore, 1; Santa Cecilia, 43.

Identification.—*Leptodeira annulata* is one of two species of snakes in the area having the dorsal scales in 19 rows and the vertebral row enlarged, although in some individuals of this species, the vertebral row is only slightly enlarged. The other is *Tripanurgos compressus*. *Leptodeira* differs from *Tripanurgos* by having a divided anal plate (single in *Tripanurgos*), one anterior temporal (two), and broad middorsal brown blotches on the body (narrow transverse blotches). Other snakes having laterally compressed bodies and enlarged vertebral scale rows have fewer rows of dorsal scales: *Imantodes cenchoa* (17), *Imantodes lentiferus* (15), and *Dipsas* (13).

The head is brown, with or without a dark brown spot or stripe on the nape; a broad, dark brown postorbital stripe is present. The dorsum is tan, grayish tan, or reddish tan with dark brown middorsal blotches extending to the fourth or

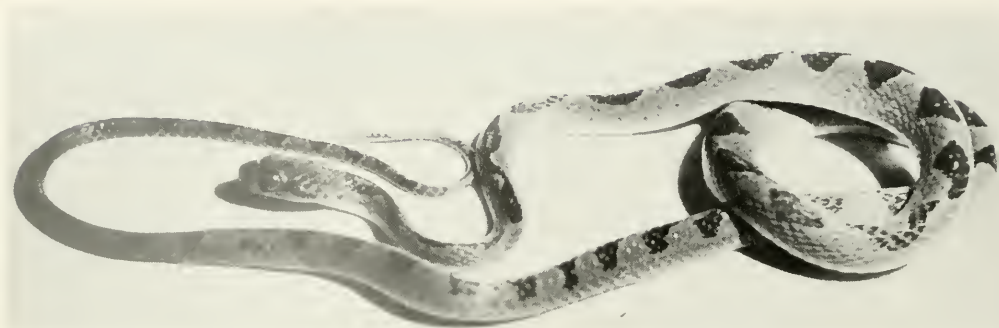


FIG. 153.—*Leptodeira annulata annulata*, ♂, 568 mm SVL (KU 109840).

fifth row of scales. The blotches usually are connected on the midline, especially anteriorly, where the confluent blotches are no more than five scales in width; thus, in many individuals the anterior pattern consists of a broad, zig-zag mid-dorsal stripe. The venter is creamy white to yellowish tan anteriorly, changing to orange-tan or pinkish tan posteriorly. The underside of the tail is brown or grayish tan. The iris is orange-tan to pale brown. In juveniles the occipital region is white. ♂ 560+171 mm; ♀ 578+182 mm.

Occurrence.—This nocturnal, arboreal, snake is most abundant in secondary forest; 78 percent were found there, whereas only 17 percent were found in primary forest. Others were found in buildings or at the edge of the forest. Most (65%) were on vegetation less than 1.5 m above the ground; others were found up to heights of 6 m. Active *Leptodeira* most frequently are observed in herbs and bushes in and around ponds where frogs are calling; 65 percent of the snakes were captured within 3 m of water. Only one individual was found by day; it was in a bromeliad on a tree limb about 2.5 m above the ground.

The monthly distribution of specimens is biased by the inequable distribution of field work, but even so there is a heavy concentration of snakes in May-July. The number of *Leptodeira* obtained throughout the year is: February (2), March (4), April (4), May (9),

June (12), July (10), August (1), October (2). Three of the snakes from July are hatchlings. Because these snakes feed almost exclusively on frogs, it might be anticipated that they are most active at times of greatest anuran breeding activity – April-May, October-November. Duellman (1958:119) showed bimodal seasonal incidence of captures of 104 *Leptodeira* at Iquitos, Perú; peaks were in March and August.

Life History.—One female collected in May contained six ovarian eggs. Three eggs from a clutch found on 5 April hatched on 10 July. The hatchlings had body lengths of 142, 145, and 146 mm. The eggs were part of a group of 15 found in a cavity of a bamboo about 12 m above the ground. No obvious differences in size or shape were noted, so it was a surprise when some hatched into *Leptodeira* and others into *Leptophis ahuetulla*. The limited data on reproduction at Santa Cecilia does not refute Duellman's (1958:115) supposition that *Leptodeira annulata* breeds throughout the year at Iquitos, Perú.

Food.—Stomach contents revealed only anuran remains: *Hyla marmorata* (2), *Hyla lanciformis* (1), *Hyla parviceps* (1), *Eleutherodactylus brevicaudus* (1), *Hyla bokermanni* (1), and *Phyllomedusa* eggs (3).

Remarks.—The relative abundance of *Leptodeira* in primary and secondary forests may be more apparent than real. Most of the snakes were found at sites

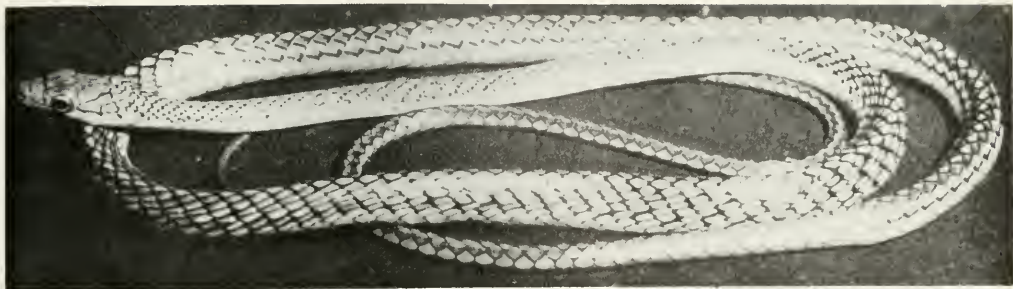


FIG. 154.—*Leptophis ahuetulla nigromarginatus*, ♀, 896 mm SVL; Limoncocha, Provincia Pastaza, Ecuador (KU 107041).

where frogs were breeding. Those sites that were worked most intensively were in secondary forest.

Leptophis ahuetulla nigromarginatus
(Günther)

(FIGURE 154)

Material.—Santa Cecilia, 15.

Identification.—*Leptophis ahuetulla* is the only long, slender snake in the area that is primarily green and has smooth dorsal scales in 15 rows at midbody. Other colubrids that are green (*Leimadophis reginae*) or have green stripes (*Oxybelis argenteus*) have dorsal scales in 17 rows. The various species of *Chironius* can be distinguished from *Leptophis* by having dorsal scales in 10 or 12 rows.

The dorsum is bright green; each of the scales on the body and plates on the head is margined with black. The first three scale rows are bronze or copper colored. The venter is metallic salmon. The iris is yellow, and the tongue is bluish green with a black tip.

The oblique scale rows and diminishing size of the scales dorsolaterally give a false impression of an enlarged vertebral scale row. In some individuals the dorsal scales on the posterior part of the body are weakly keeled. ♂ 662+433 mm; ♀ 620+398 mm.

Occurrence.—We have limited ecological data from Santa Cecilia, but observations there and elsewhere reveal that *L. ahuetulla* is diurnal, and arboreal,

mostly in low, dense vegetation in primary and secondary forest.

Life History.—A female collected in April contained one egg 16.2 mm in length, and a female from July contained three eggs 18.1 mm in length. Fifteen eggs were found in a cavity of a bamboo about 12 m above the ground on 5 April. Four of these hatched between 10 and 17 May; four others hatched between 26 June and 1 July. Three of the entire clutch hatched into *Leptodeira*. The remaining eggs spoiled. Apparently the composite nest contained not only eggs of two species but also clutches of *Leptophis* eggs laid more than a month apart. Body length of eight hatchlings is 142–146 ($\bar{x}=157.5$) mm, and tail length of 92–105 ($\bar{x}=98.4$) mm. The limited reproductive data from Santa Cecilia supports Oliver's (1947:5) contention that this species reproduces throughout the year at Iquitos, Perú.

Food.—One individual had eaten two *Hyla alboguttata*.

Taxonomic Comments.—Juveniles and some adults have extensive coppery coloration on the body; thus, they resemble *Leptophis cupreus* (Cope), as defined by Peters and Orces-V (1960). Examination of 18 specimens from provincia Napo revealed the following variation: ventrals, ♂♂ 147–155 ($\bar{x}=149.9$, $N=7$), ♀♀ 149–157 ($\bar{x}=153.3$, $N=11$); subcaudals ♂♂ 144–154 ($\bar{x}=148.8$, $N=7$), ♀♀ 137–159 ($\bar{x}=148.9$, $N=8$); caudal reduction from six to four rows at level of subcaudal 2–6 ($\bar{x}=5.0$, $N=18$);



FIG. 155.—*Liophis cobella*, ♀, 522 mm SVL (KU 126043).

upper labials 8-9 ($\bar{x}=8.5$, $N=18$); preocular in contact with frontal in two of 18 specimens. In all of these characters the sample from Santa Cecilia is much more like *L. alhuettulla* than *L. cupreus* (see Peters and Orces-V, 1960, for diagnoses).

Liophis cobella (Linnaeus)
(FIGURE 155)

Material.—Santa Cecilia, 2.

Identification.—*Liophis cobella* is a predominantly tan snake with dark brown dorsal blotches, some of which extend across the venter. It is most easily confused with *Atractus major* which has a single anal plate (divided in *Liophis*) and dorsal blotches that do not extend across the venter. Other similarly patterned snakes are the species of *Helicops*, and *Drymobius*, which have keeled scales in 19 or 21 rows at midbody. Other snakes having smooth dorsal scales in 17 rows and a divided anal are *Rhadinæa* and *Leimadophis*, neither of which has large dorsal blotches extending across the venter.

The dorsal ground color is tan; about 40 dorsal dark brown blotches are present on the body; most of these alternate but connect with large lateral blotches which extend as black bars one or two ventrals wide across the belly. The lips are grayish brown; the chin and throat are cream. The belly is tan with a suf-

fusion of salmon, and the underside of the tail is cream. The iris is reddish brown, and the iris is red with a black tip. ♀ 525+109 mm.

Occurrence.—One was on the ground in a clearing at night and one in a water-filled, grassy depression in a clearing at night.

Life History.—A female from April contained six oviducal eggs 25.1 mm in length.

Ninia hudsoni Parker
(FIGURE 156)

Material.—Puerto Libre, 1.

Identification.—This small snake is the only species in the area having dorsal scales keeled and in 21 rows throughout the length of the body. The much larger *Pseustes sulphureus* has 21 rows at midbody; the number of rows is reduced to 13 or 15 anterior to the anus. In coloration, *Ninia hudsoni* is unique in having a dark gray dorsum with a pale gray nape band and a creamy white venter. The pattern of some *Atractus occipitoalbus* is similar, but in these the belly also is dark gray. Furthermore, *A. occipitoalbus* has smooth dorsal scales in 15 rows. ♀ 326+83 mm.

Occurrence.—The single specimen was beneath a fallen palm frond in primary forest by day.

Life History.—The single female col-



FIG. 156.—*Ninia hudsoni*, ♀, 409 mm SVL (KU 121913).

lected in July contained two oviducal eggs 20.6 mm in length.

Remarks.—As in the case of many other secretive snakes, it is unknown whether *Ninia hudsoni* is diurnal or nocturnal. In reference to *Ninia sebae sebae* (Duméril and Bibron) in Alta Verapaz, Guatemala, Stuart (1948:77) stated: "This snake seems to pass its entire life in concealment, and it was only occasionally that it could be found on the surface of the ground even at night."

Oxybelis argenteus (Daudin)

(FIGURE 157)

Material.—Santa Cecilia, 50.

Identification.—This elongate, slender snake with a round body and long, pointed snout is easily distinguished from other snakes in the area by its shape and coloration – dull green and tan stripes dorsally and green and white stripes ventrally. No other snakes are so colored.

Leptophis ahuetulla also is slender and round, but it is predominantly green dorsally and has dorsal scales in 15 rows (17 in *Oxybelis*). The various nocturnal tree snakes, (*Dipsas*, *Imantodes*, *Leptodeira*, *Tripanurgos*) with slender bodies have laterally compressed bodies, blunt heads, and blotched dorsal patterns.

The top of the head is brown, and the dorsum of the body is tan with three dull green stripes. The throat, lower labials, and anterior part of the belly are pale lime green with brown or black flecks. The rest of the venter is white with two green stripes, which are darkest posteriorly. The iris is pale yellow with a median brown streak. The tongue is olive-brown above and yellow below. ♂ 774+508 mm; ♀ 787+548 mm.

Occurrence.—This is the most abundant snake in our collections. Specimens were obtained every month except December; five or more were collected in February, March, June, July, and Au-

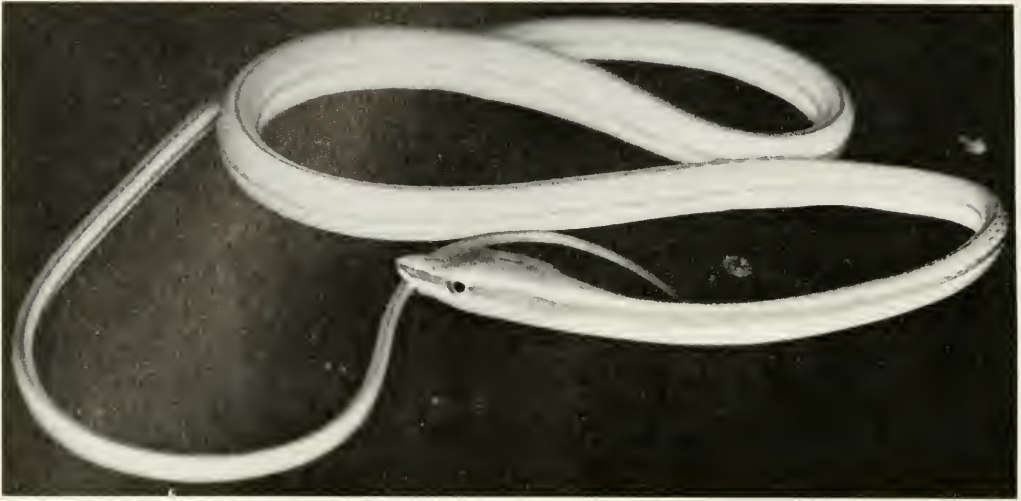


FIG. 157.—*Oxybelis argenteus*, juvenile, 412 mm SVL (KU 112280).

gust. Only three individuals were found by day – in grassy clearing, on low bush, and on vine-covered tree trunk. All others were sleeping on bushes and trees at night. Most of these (77%) were on vegetation less than 1.5 m above the ground. Although some sleeping snakes were loosely coiled on leaves or draped on branches or vines, one sleeping posture was most often seen. The snakes coil rather tightly around a small vertical branch or twig rising from a horizontal branch. Approximately 80 percent of *Oxybelis* were found in second growth forest; the others were in primary forest (12%) or forest edge (8%).

Apparently with increased human disturbance resulting in more secondary type forest the species is increasing in abundance. We have ecological data and dates of collection for 41 *Oxybelis* from Santa Cecilia. The number of specimens obtained in each year is shown as the number in primary forest:secondary forest:forest edge – 1966 (0:0:1), 1967 (2:0:1), 1968 (4:0:0), 1969 (0:0:1), 1971 (0:8:1), 1972 (0:17:0), 1973 (0:4:0).

Life History.—One female from July contained four oviducal eggs 33.4 mm in length, and one from August contained

three maturing ovarian eggs 23.7 mm in length. In the second week of July a female deposited six adherent eggs (12-14, $\bar{x}$ =12.8 mm in diameter; 31-36, $\bar{x}$ =32.7 mm in length). The smallest juveniles, having body lengths of 143 and 191 mm, were found in April and October, respectively.

Food.—The stomachs of 10 individuals contained food representing two species of lizards and three of frogs. The most abundant food items were *Prionodactylus argulus* and *Eleutherodactylus variabilis* (3 each). Also eaten were *Anolis trachyderma* (2), *Dendrophryniscus minutus* (1), and *Eleutherodactylus pseudoacuminatus* (1). Although *Prionodactylus argulus* is primarily a leaf-litter inhabitant, individuals do ascend bushes, where some fall prey to *Oxybelis*. *Anolis trachyderma* and the two species of *Eleutherodactylus* are bush inhabitants. Although the *Eleutherodactylus* are primarily nocturnal, occasional individuals were active after diurnal rains, and *E. variabilis* calls from shaded areas in the late afternoon. Perhaps *Oxybelis* finds sleeping individuals by day. *Dendrophryniscus* lives on the forest floor; the presence of that species in the stomach of an *Oxybelis* is indica-

tive that these arboreal snakes occasionally feed on the ground. Also, perhaps some of the *Prionodactylus* were eaten on the ground.

Oxyrhopus formosus (Weid)

Material.—Lago Agrio, 1; Puerto Libre, 1; Santa Cecilia, 3.

Identification.—Among the several species of colubrid snakes in the area that have a black and white (or yellow) head and red body, at least in some stage of growth, *Oxyrhopus formosus* is unique in having banded juveniles and unicolor adults. In juveniles (< 250 mm body length), the tip of the snout is cream, the top of the head is tan, and the head posterior to the eyes and the nape are creamy yellow. The body and tail are creamy yellow with 17-20 broad black blotches that are slightly narrower laterally than middorsally and extend onto the edges of the ventrals and are complete across the ventral surface of the tail. The blotches are 5-10 scales in length; the intervening cream areas are 2-3 scales in length. Half-grown individuals (400-500 mm body length) have a cream snout including the entire area anterior to the eyes; the top of the head is brown, and the cream nape band is suffused with brown. The posterior tips of all dorsal scales are dark or black. The blotches are dull reddish brown, and the interspaces are pinkish cream. In adults (> 620 mm in body length) the snout anterior to the eyes and the upper labials are creamy yellow; the rest of the head and the nape are dark brown or black. The dorsum of the body and tail is pale salmon red; the tips of the scales are black. The venter in juveniles is cream; in adults it is pinkish salmon.

Juveniles are easily confused with *Oxyrhopus petola*, but in that species the snout is black and the body blotches are longer (8-12 scales). Furthermore, *O. petola* has more ventrals and subcaudals (Table 9) and does not have the preocular in contact with the frontal. The col-

oration of adult *O. formosus* resembles that of *Clelia clelia*, *Drepanoides anomalous* and *Pseudoboa coronata*. *Clelia* has a black snout and more ventrals and subcaudals (Table 9). *Drepanoides* has dorsal scales in 15 rows and *Pseudoboa* in 17 rows; both have black snouts and broad cream bands across the head posterior to the eyes.

One specimen (KU 126017) has 21 rows of scales at midbody; all others have 19 rows. The iris is reddish tan to rusty red, and the tongue is black. ♂ 621+198 mm; ♀ 830+197 mm.

Occurrence.—One was moving on the ground in primary forest at night, and one was obtained during clearing of primary forest by day.

Life History.—Two females from May having body lengths of 778 and 830 mm contained 17 and 13 maturing ova, respectively.

Food.—One individual contained a diurnal, teiid lizard *Arthrosaura reticulata*.

Oxyrhopus melanogenys (Tschudi)

Material.—Santa Cecilia, 12.

Identification.—This predominantly black or dark gray snake has smooth dorsal scales in 19 rows at midbody. The head is black bordered posteriorly by an orange or red nape band. The body pattern consists of broad (6-13 scales), black bands that extend well onto the ventrals, especially posteriorly. The bands are separated anteriorly by narrow (1-2 scales), sometimes incomplete, white or pale yellow interspaces. On the posterior half of the body the pattern is tricolor: black-yellow-black-red-black-yellow-black. The red bands vary from orange to dull red and are 3-5 scales wide. The red bands are suffused with black; in large adults the bordering black bands meet middorsally, thereby restricting the red band to a pair of lateral spots. One or two red bands are present proximally on the tail, which is black posteriorly. The chin and belly are dull

cream; the underside of the tail is black. In one individual the normally white interspaces are lime green. The iris is reddish brown, and the tongue is dark gray with a white tip. ♂ 629+187 mm; ♀ 819+199 mm.

The only other *Oxyrhopus* likely to be confused with *O. melanogenys* is *O. petola*. However, that species has black and red (yellow in juveniles) bands throughout the length of the body and more ventrals and subcaudals (Table 9). Triads of black, red, and yellow rings occur in *Atractus elaps*, *Erythrolamprus aesculapii*, and some species of *Micrurus*, but in all of these the pattern is present throughout the length of the body, and the rings are continuous across the venter.

Occurrence.—Five were active on the ground in clearings by day; two were moving on the ground in clearings at night. One was coiled in the crotch of a small tree at night, and another was under a log in a clearing by day. These observations and the nature of the food found in the stomachs indicate that this species is primarily diurnal.

Life History.—One female from April with a body length of 819 mm contained 12 small ova.

Food.—Stomach contents consisted of one small rodent and three diurnal teiid lizards, *Arthrosaura reticulata*, *Iphisa elegans*, and *Lepsoma parietale*.

Oxyrhopus petola digitalis (Reuss)

Material.—Puerto Libre, 1; Santa Cecilia, 20.

Identification.—This snake has smooth dorsal scales in 19 rows and a pattern of broad black blotches on the dorsum of the body and tail. The snout and head are black; there are 12-17 ($\bar{x}$ =15.1, N =18) black bands 8-12 scales wide on the body. The bands extend onto the edges of the ventrals and are separated by pale interspaces 2-3 scales wide middorsally and 4-5 scales wide laterally. In most individuals, some black bands are offset

at the midline, especially at midbody. The chin, lower labials (but not upper labials), ventrals, and subcaudals are creamy yellow. In juveniles (< 300 mm body length) the nape band and interspaces are pale yellow. The interspaces become orange and then red progressing anteriorly in larger individuals. Snakes having body lengths of 350-450 mm have red interspaces posteriorly, orange ones at midbody and anteriorly, and a yellow nape band. Snakes with body lengths less than 525 mm have red interspaces and a yellow nape band; in larger individuals the nape band is red. The red is darkest in larger individuals. In juveniles the ventral surface of the tail is immaculate, but in larger individuals an irregular, midventral black line is present. The iris is brown, and the tongue is gray. ♂ 622+218 mm; ♀ 557+211 mm.

This snake can be confused with juveniles of *Oxyrophus formosus*, but in that species the snout is cream, the black bands are shorter (5-10 scales), and the interspaces are creamy yellow. Furthermore, *O. formosus* has fewer ventrals and subcaudals (Table 9) and does not have the preocular in contact with the frontal. *Oxyrhopus petola* can be distinguished readily from *O. melanogenys* in that the latter has narrow (1-2 scales) yellow interspaces separating broad (6-13 scales) black bands anteriorly and a tricolor pattern posteriorly: black-yellow-black-red-black-yellow-black. Moreover, *O. melanogenys* has fewer ventrals and subcaudals (Table 9).

Occurrence.—Five individuals are from forest, the others from clearings. Five were moving at night; one was coiled in a bush in a swamp and another on a low bush in forest at night. Others were active on the ground by day. Apparently this species is primarily nocturnal.

Life History.—No data are available from Santa Cecilia. Fitch (1970:154) reported seven gravid females from Iquitos, Perú, having 5-10 ($\bar{x}$ =7.3) eggs col-

lected in March, September, and November.

Food.—Two individuals contained diurnal, terrestrial teiid lizards, *Kentropyx pelviceps* and *Prionodactylus manicatus*.

Pseudoboa coronata Schneider

Material.—Santa Cecilia, 7.

Identification.—This red snake with a black and cream head differs from other similarly colored snakes by having single, instead of divided, subcaudals. Other snakes in the area with similar color patterns are *Clelia clelia*, *Oxyrhopus formosus*, and *Drepanoides anomalus*. The latter has dorsal scales in 15 rows, and the others have 19 rows, whereas *Pseudoboa* has 17 rows.

The anterior part of the head, including the eyes, is black; the rest of the head and anterior part of the neck are creamy white. A diffuse back band separates the creamy white neck from the red body. The tips of the dorsal scales are black, more so in adults than in juveniles. The venter is cream. ♀ 816+245 mm.

Occurrence.—One was in water in a muddy depression in secondary forest at night. Two were active on the ground in clearings by day and one at night. The stomach contents suggest that this species may be primarily diurnal.

Life History.—One female collected in September with a body length of 761 mm contained four oviducal eggs 34.2 mm in length.

Food.—Two individuals contained diurnal, teiid lizards, *Ameiva ameiva*, and one contained remains of two juvenile rodents.

Pseustes sulphureus sulphureus (Wagler)

Material.—Santa Cecilia, 1.

Identification.—This large snake has keeled dorsal scales in 21 oblique rows at midbody, that are reduced to 13 rows anterior to the anus, and a single anal plate. Two other snakes in the area have keeled dorsal scales in 21 rows at mid-

body. *Ninia hudsoni* is dark gray with a pale band on the head, and *Helicops petersi* has fused internasals and about 40 middorsal dark blotches alternating with lateral blotches. *Pseustes* has paired internasals and no blotches anteriorly on the body and indistinct transverse blotches posteriorly. *Xenodon severus* also has 21 oblique rows of dorsals at midbody, but in *Xenodon* the scales are smooth, and the anal plate is divided.

The dorsum is dull olive-green, and the skin between the scales is yellow anteriorly and gray posteriorly. Transverse marks on the posterior part of the body are black. The chin and throat are bright lemon yellow tinged with olive. The anterior fourth of the belly is dull olive tinged with yellow, and the rest of the venter is gray tinged with olive. The iris is dull brown, and the tongue is pink with an orange tip. ♂ 1328+455 mm.

Occurrence.—The single specimen was brought in by an Indian, who said he found it on the forest floor by day.

Life History.—No data are available.

Food.—The specimen contained a rodent.

Rhadinaea brevirostris (Peters)

(FIGURE 158)

Material.—Lago Agrio, 1; Santa Cecilia, 7.

Identification.—The presence of smooth dorsal scales in 17 rows at midbody and a divided anal plate distinguish *Rhadinaea* from all other snakes in the area, except *Leimadophis* and *Liophis*. *Rhadinaea* has dark and light brown dorsal stripes and an immaculate belly. *Leimadophis* is tan or brown with or without lateral stripes posteriorly and with black spots on the belly. *Liophis* has dark brown bands complete around the body. The coloration of *Rhadinaea* is similar to that of *Tantilla melanocephala*, which lacks a loreal and has a narrow (1 scale row wide) middorsal brown stripe. *Rhadinaea* has a loreal and a middorsal brown stripe three scales in width.

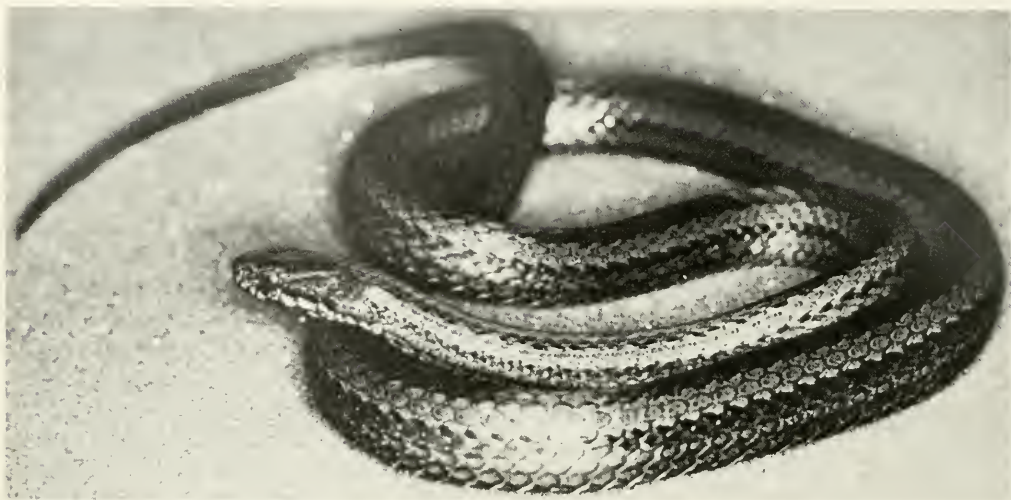


FIG. 158.—*Rhadinaca brevirostris*, ♀, 419 mm SVL (KU 119391).

The head is dark brown with reddish tan spots; the upper labials are creamy tan with brown flecks. The dorsum of the body is pale brown or grayish tan. Five dark brown stripes extend the length of the body – lateral pair on edges of ventrals, dorsolateral pair on lower edge of fifth scale row, and dorsal on vertebral and paravertebral rows. In some individuals the dorsolateral stripe is narrowly bordered above by a narrow creamy tan stripe. The chin is reddish tan to cream, and the belly is creamy white (pale green in one of five adult females). The iris is pale brown with a narrow red ring around the pupil. ♂ 300+91 mm; ♀ 269+86 mm.

Occurrence.—This small, diurnal snake was found in a variety of terrestrial situations – primary and secondary forest, clearing, and banana grove. Three are from May, two from August, and one each from June, July, and November.

Life History.—One female collected in May contained two oviducal eggs 26.2 mm in length.

Food.—One individual contained a teiid lizard, *Prionodactylus manicatus*.

Siphlophis cervinus (Laurenti)

Material.—Santa Cecilia, 2.

Identification.—Smooth dorsal scales in 19 rows at midbody, a single anal plate, and two anterior temporals distinguish *Siphlophis* from all other snakes in the area. Furthermore, the species has a distinctive color pattern. The sides of the body are pale yellow with 75-80 irregular, vertical black marks, each slightly wider than adjacent interspaces. A diffuse, orange-red middorsal stripe extends the length of the body. The top of the head and the iris are brown. The throat is pale gray, and the rest of the venter is pale yellow. The tongue is pale pink. ♂ 551+188 mm.

Occurrence.—One individual of this nocturnal snake was under a rock in a clearing by day; the other specimen lacks ecological data.

Life History.—No data are available.

Food.—One had eaten a teiid lizard, *Bachia trinasale*.

Tantilla melanocephala melanocephala (Linnaeus) (FIGURE 159)

Material.—Lago Agrio, 3; Santa Cecilia, 2.

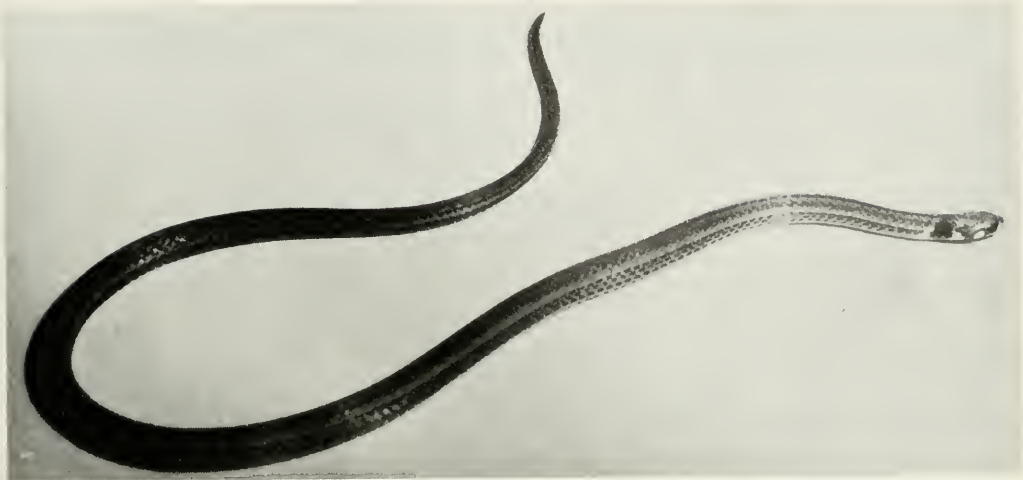


FIG. 159.—*Tantilla melanocephala melanocephala*, ♂, 309 mm SVL (KU 109848).

Identification.—This small brown snake has smooth dorsal scales in 15 rows throughout the length of the body. The anal plate is divided, and the loreal is absent. The only other snake in the area with a divided anal plate, no loreal, and smooth dorsals in 15 rows is *Leptophis ahuetulla*, a long green snake with only 11 or 13 rows of scales posteriorly. *Tantilla* superficially resembles *Rhadinæa brevirostris*, which has 17 rows of scales at midbody, a loreal, and a broad (3 scales in width) dark brown middorsal stripe. In *Tantilla* the middorsal stripe is only one scale wide. *Tantilla* with dull patterns might be confused with the brown phase of *Atractus occipitoalbus* which has a single anal, no mid-dorsal dark stripe and has a midventral row of dark spots.

The top of the head is brown. A broad dark brown nape band is bordered laterally by cream spots. A narrow (1 scale wide) dark brown stripe extends from the nape band to the tip of the tail. A dark brown lateral stripe on dorsal scale rows 1 and 2 is bordered above on the anterior part of the body by a narrow tan stripe; the rest of the dorsum is brown. The side of the head is dark brown with white labial spots anterior and posterior to the orbit. The lower

labials are dark brown and white. The chin and throat are white, and the belly and underside of the tail are pale green or greenish cream. The iris is orange-tan above and grayish brown below; the tongue is brown with a white tip. ♂ 253+82 mm; ♀ 207+16+ mm (incomplete).

Occurrence.—All specimens were active on the ground or amidst leaf litter in primary forest by day. Three were obtained in May and one each in March and August.

Life History.—The single female collected in May showed no evidence of reproductive activity.

Taxonomic Comments.—Schmidt and Walker (1934b:318) referred populations of *Tantilla melanocephala* from coastal Perú and the upper Marañón valley of Perú to *T. melanocephala capistrata* Cope and distinguished the two subspecies by the contact of the prefrontal with the second upper labial in *capistrata* and no contact in *melanocephala*. Peters and Orejas-Miranda (1970:295) noted that in *capistrata* the tip of the snout is white and in *melanocephala*, brown. All of the specimens from Santa Cecilia and Lago Agrio have brown snouts; in two, the prefrontals are in contact with the upper labials on both

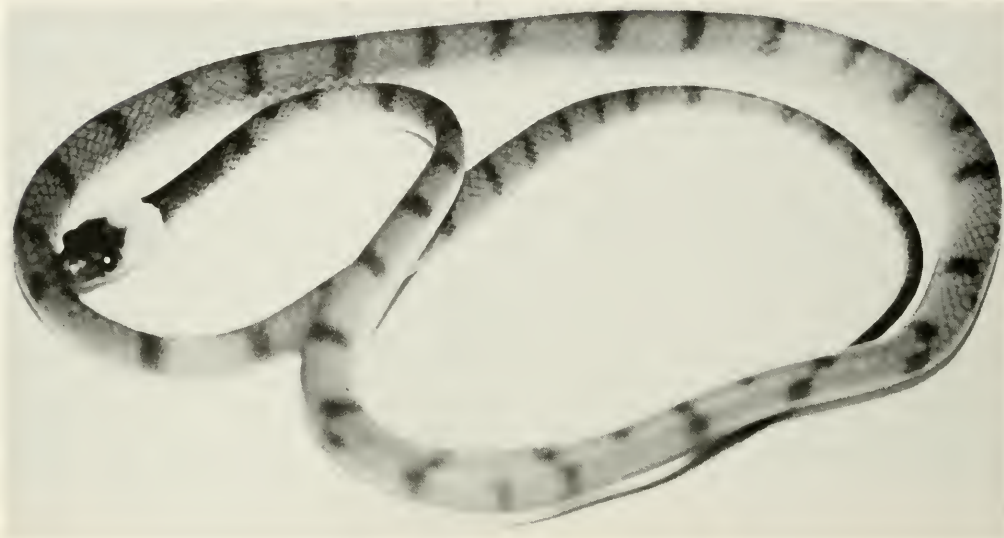


FIG. 160.—*Tripanurgos compressus*, ♀, 582 mm SVL (KU 148395).

sides, and in one, there is contact only on one side, whereas in the others the prefrontal is separated from the upper labials.

***Tripanurgos compressus* (Daudin)**

(FIGURE 160)

Material.—Lago Agrio, 1; Santa Cecilia, 1.

Identification.—This is one of two snakes in the area with dorsal scales in 19 rows and an enlarged vertebral scale row. The other is *Leptodeira annulata*, which differs by having a divided anal plate (single in *Tripanurgos*), one anterior temporal (two), and broad mid-dorsal brown blotches on the body (narrow transverse blotches). Other snakes having laterally compressed bodies and enlarged vertebral scale rows have fewer rows of dorsal scales: *Imantodes cenchoa* (17), *Imantodes lentiferus* (15), and *Dipsas* (13).

The head is dark brown bordered posteriorly by a pale yellow nape band and a dark brown band. The dorsum of the body is reddish brown with about 45 narrow dark brown marks one or two

scales in length and extending laterally to the first or second scale row. The venter is creamy tan. The iris is burnt orange. ♀ 612+87 mm.

Occurrence.—One specimen was retrieved from a large tree when it was felled in primary forest by day in May. The other was crawling in low vegetation in secondary forest at night in March.

Life History.—No data are available.

Food.—One individual contained the remains of a microteiid lizard.

***Xenodon severus* (Linnaeus)**

(FIGURE 161)

Material.—Puerto Libre, 2; Santa Cecilia, 6.

Identification.—*Xenodon severus* is the only snake in the area having smooth dorsal scales in 21 oblique rows. The body is heavy and depressed; the anal plate is single, and one anterior temporal is present. Other snakes in the area with 21 rows of scales at midbody (*Helicops*, *Ninia*, and *Pseustes*) all have keeled scales, except that some specimens of *Oxyrhopus formosus* have 21 rows of smooth scales. *Oxyrhopus formosus* is a

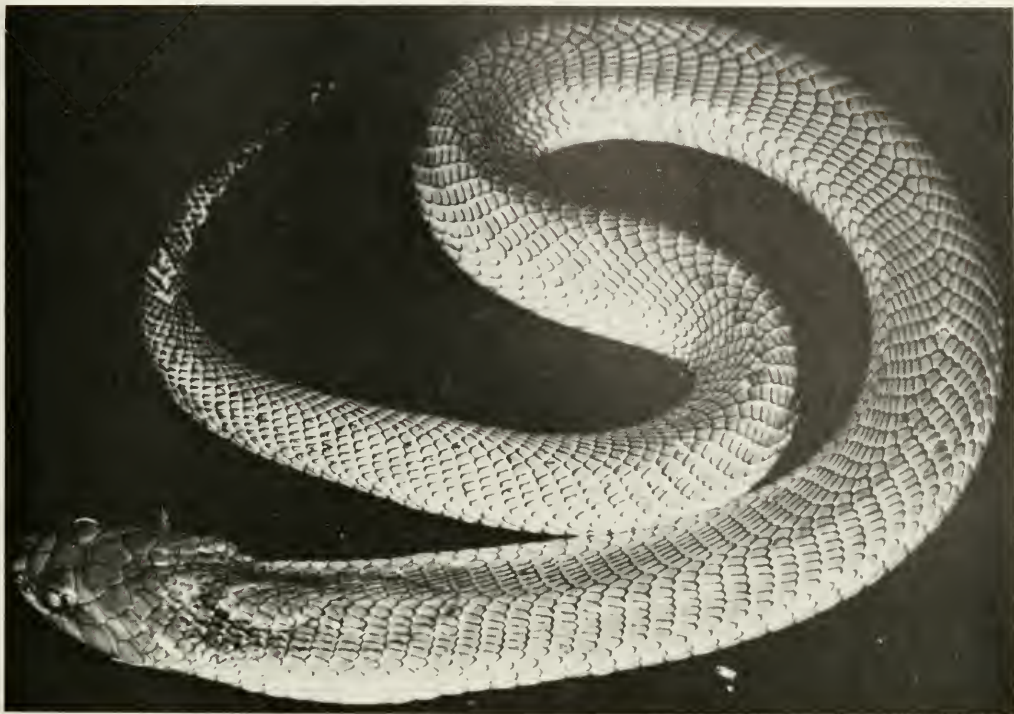


FIG. 161.—*Xenodon severus*, ♂, 880 mm SVL (KU 121927).

slender, round-bodied snake with two anterior temporals, dorsals in diagonal rows, and a color pattern entirely different from that of *Xenodon*.

Ontogenetic change in coloration results in a nearly uniformly colored adult from a banded juvenile. Small juveniles (< 300 mm body length) have a pattern of diagonal dark brown and grayish white markings on the head. The tip of the snout is brown, outlined in white. A brown bar is continuous across the internasals and thence posteriorly through the orbit to the ventrolateral surface of the neck; it is bordered by white bars, the upper of which continues posteriorly on the side of the neck. A dark brown interorbital bar is narrowly connected middorsally on the frontal to the anterior end of a large ovoid brown blotch that continues onto the anterior part of the body. On the nape the middle of the blotch has a large tan spot. The dorsum of the body is tan with 6-8 brown

blotches outlined in black. The blotches are 10-14 scales in length and extend laterally onto the first scale row. The interspaces are tan and 3-4 scales in length. The venter is dark brown with creamy yellow spots laterally.

In larger individuals (< 700 mm), the markings become diffuse, and the dorsum is olive-tan or yellowish tan. The ovoid spot with a pale center on the head and neck persists; it is especially evident when the body is flattened, and the neck is spread. In large adults the body is dark gray or black with yellowish tan scales forming incomplete, irregular transverse lines posteriorly in some specimens. The head is brown, and the lower labials and throat are yellow. The belly is creamy yellow to orange-tan. The iris is brown, and the tongue is flesh-colored with a gray tip. ♂ 807+139 mm; ♀ 1060+152 mm.

Occurrence.—This diurnal, terrestrial snake inhabits both primary and second-

dary forest. Two were obtained in each of May, June, and July; one was obtained each in February and August.

Life History.—One female collected in May contained 22 ova. Fitch (1970: 173) noted that the species "seems to have year-round breeding in the tropical equatorial lowlands."

Food.—*Xenodon serverus* is a prodigious frog eater. Two individuals contained *Bufo marinus*, and two contained *Leptodactylus pentadactylus*. One individual (body length 1050 mm) was found in the process of eating a *L. pentadactylus* having a snout-vent length of 173 mm; subsequent examination revealed one adult *L. pentadactylus* already in the stomach.

Just how *Xenodon* ferrets out large frogs by day is not known. Neither the feeding individual, nor others containing food, was taken immediately after heavy rains.

Xenopholis scalaris (Wucherer)

Material.—Lago Agrio, 1; Puerto Libre, 1; Santa Cecilia, 1.

Identification.—This small snake is distinctive in having the prefrontals fused into a single large shield. The dorsal scales are smooth and in 17 rows. The dorsum is reddish brown becoming pinkish orange or orange-tan laterally. There are 24-30 narrow black crossbars on the body; these extend laterally onto the third or fourth scale row. In some individuals the bars are offset middorsally and/or connected by a narrow middorsal line. The crossbars are 1-2½ scales wide. Small black flecks are present on the first and second rows of dorsal scales. The ventral surfaces are immaculate creamy white. The iris is dark reddish brown, and the tongue is pink. ♂ 244+54 mm; ♀ 317+56 mm.

Occurrence.—All were found by day. One was moving in a clearing; two were in primary forest — one under a palm frond and one in leaf litter.

Life History.—A female obtained in

May contained three oviducal eggs 23.9 mm long.

Food.—One individual contained a terrestrial frog, *Ischnocnema quixensis*.

ELAPIDAE

Leptomicrurus narduccii (Jan)

(FIGURE 162)

Material.—Lago Agrio, 1; Santa Cecilia, 4.

Identification.—This long, slender snake has a round body, blunt head, and short tail. It is uniformly black above except for a bright yellow band around the head. Ventrally it is black with large yellow spots; the spot (or spots) on the ventral surface of the tail is orange or red. In freshly preserved specimens, the spots on the belly are red. Only two other snakes in the area are dark above and have a pale band on the head or neck. Of these, *Atractus occipitoalbus* is like *Leptomicrurus* in having smooth dorsal scales in 15 rows, but in *Atractus* the venter is uniform gray and the band on the occiput is dull orange to pinkish orange. The other species is *Ninia Hudsoni*, which has keeled dorsal scales in 21 rows, a pale gray band across the neck, and a creamy white venter. ♂ 893+43 mm; ♀ 798+34 mm.

Occurrence.—One was beneath a log in primary forest, and another was plowed up by a bulldozer during the clearing of mature forest.

Life History.—One female collected in May contained small ovarian eggs.

Remarks.—When disturbed, one individual spiraled the tail dorsally, revealing the ventral red markings.

Micrurus langsdorffi langsdorffi Wagler

(PLATE 4)

Material.—Lago Agrio, 1; Santa Cecilia, 1.

Identification.—This distinctive coral snake differs from other *Micrurus* and coral snake mimics in the area by having numerous (36-38) narrow black rings



FIG. 162.—*Leptomocurus narduccii*, ♀, 605 mm SVL (KU 126057).

not arranged in triads, and bordered by narrow white rings. The red rings are not more than five scales wide. The snout and top of the head are black. The other species of *Micrurus* have black rings in triads: black-yellow-black-red-black-yellow-black. In *M. langsdorffi* the rings are black-white-red-white-black. Some *Atractus elaps* have a pattern like that of *M. langsdorffi*, but the former has much wider red rings, fewer than 20 black rings, single anal plate, and only one pair of chinshields; *M. langsdorffi* has a divided anal plate and two pairs of chinshields. *Anilius scytale*, which is red with about 50 black rings, differs by having the eye beneath a single scale, only five enlarged head shields, and ventral scutes only slightly wider than the dorsal scales, whereas *M. langsdorffi* has the eye surrounded by several scales, seven enlarged dorsal head shields, and enlarged ventral scutes.

The white rings usually are no more than one-half scale in width. The red rings are dark red, and the scales in the red rings are tipped with black. The chin is white. ♂ 483+91 mm; ♀ 676+65 mm.

Occurrence.—One individual was crawling on the ground in a clearing by day; another was killed by natives by day.

Life History.—A female obtained in May contained small ovarian eggs.

Micrurus lemniscatus helleri
Schmidt and Schmidt

(PLATE 4)

Material.—Lago Agrio, 1; Santa Cecilia, 2.

Identification.—Three species of *Micrurus* in the area have a pattern of rings arranged in triads: black-yellow-black-red-black-yellow-black. Of these, *M. lemniscatus* is the only species having a ringed pattern on the head; the snout is black, followed successively by yellow, black, and yellow rings, and a black nape. In *M. spixii* the head and nape are black; in *M. surinamensis* the head scutes are black and red. *Erythrolamprus aesculapii* has a ringed pattern on the head; the snout is yellow followed by a black ring, a yellow ring, and a black nape. In *Erythrolamprus* the yellow ring is posterior to the eyes, whereas in *M. lemniscatus* the yellow ring is anterior to the eyes. Some individuals of *Atractus elaps* have rings in triads, but this species has a black head with or without a creamy yellow ring posteriorly on the head and red nape.

The red rings (orange-red in life) and black rings are about equal in width (4-6 scales); the creamy yellow rings are one or two scales in width. The rings on the head is pale yellow. Few scales in the red rings have black tips. ♂ 1035+110 mm.

Occurrence.—Two were in primary forest and one in secondary forest. One was found in a trench in early evening, so the snake might have fallen in the trench by day; the other individuals were active on the forest floor by day.

Life History.—No data are available.

Micrurus spixii obscurus Jan
(PLATE 4)

Material.—Santa Cecilia, 7.

Identification.—Of the three species

of *Micrurus* having rings in triads (black-yellow-black-red-black-yellow-black), *M. spixii* is distinctive because the yellow rings are as wide as adjacent black rings (5-6 scales). *Micrurus lemniscatus* and *M. surinamensis* have yellow rings much narrower than the black rings. Furthermore, in *M. spixii* the top of the head is black, whereas *M. lemniscatus* has a yellow ring on the head, and *M. surinamensis* has black and red scales on the top of the head. Other snakes in the area having red, black, and yellow rings and dorsal scales in 15 rows include *Erythrolamprus aesculapii* and some *Atractus elaps*. The former has a yellow snout and black and yellow rings on the head. *Atractus elaps* has a single anal plate and one pair of chinshields, whereas *M. spixii* has a divided anal plate and two pairs of chinshields.

The red rings are coral red in life, and the dorsal scales in the red and pale yellow rings are suffused with black, especially middorsally. A red mark posterior to the eye includes the posterior labials and temporals. ♂ 1299+70; ♀ 778+43 mm.

Occurrence.—One was on the ground at the edge of the forest by day. All others were brought in by natives who indicated that the snakes were found on the forest floor by day.

Life History.—A female obtained in July contained small ovarian eggs.

Micrurus surinamensis surinamensis
(Cuvier)
(PLATE 4)

Material.—Santa Cecilia, 1.

Identification.—This coral snake differs from other *Micrurus* and coral snake mimics by having extremely small eyes directed anterolaterally, a small frontal, fourth upper labial barely entering the orbit, and huge anterior and posterior temporals. The head is black with dull red on the anterior edges of the scales. A narrow creamy yellow ring separates the head and body patterns. The latter

consists of six triads: black-yellow-black-red-black-yellow-black. The outermost black rings are much wider than the others (9-10 scales middorsally); the next widest are the red rings (6-7 scales), innermost black rings (4 scales), and the yellow rings (1-1½ scales). The yellow rings are expanded ventrally at the expense of the outermost black rings to include three or four ventrals. The tips of the dorsal scales in the red rings are black. ♂ 1115+147+ mm (incomplete).

Occurrence.—The single specimen was brought in by an Indian, who referred to it as *culebra del agua* (water snake). A snake, presumably the same species, was seen by day in a small stream in a clearing.

Life History.—No data are available.

Food.—According to Terry D. Schwaner (pers. com.), this specimen contained fish vertebrae in its stomach. Schmidt (1952:32) reported a small eel, *Synbranchus marmoratus*, in the stomach of an individual from Iquitos, Perú. These food items, together with the observation at Santa Cecilia and the depressed head with modified cephalic scutellation, are indicative of aquatic habits. In fact, this species of *Micrurus* is like *Hydrops triangularis* in scutellation and habitus.

Taxonomic Comments.—The present specimen (AUM 8636) is notably larger than the maximum of 1105 mm total length reported by Schmidt (1952:31).

CROTALIDAE

***Bothrops atrox* (Linnaeus)**
(FIGURE 163)

Material.—Dureno, 2; Lago Agrio, 1; Puerto Libre, 3; Santa Cecilia, 30.

Identification.—This is the most variable pit viper in the area. It differs from *Lachesis muta* in having 25, instead of 35, rows of dorsal scales at midbody and two, instead of four or five, rows of scales between the labials and the orbit. The

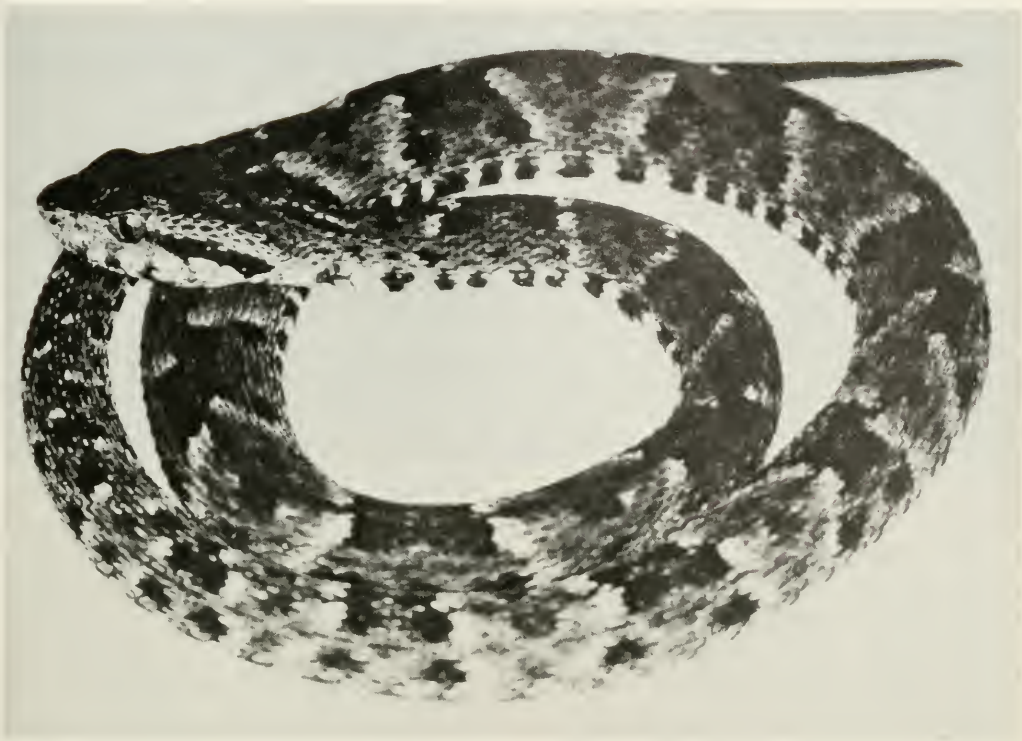


FIG. 163.—*Bothrops atrox*, juvenile, 470 mm SVL (KU 121935).

dorsal color pattern consists of irregular dark brown blotches on a tan or brown ground color. The other two species of *Bothrops* in the area differ markedly in coloration; *B. bilineatus* is green with a pale ventrolateral stripe, and *B. castelnaudi* is greenish yellow with chocolate brown blotches.

In adults and juveniles, the dorsum is dull yellowish brown, grayish brown, or brown with darker brown or black irregular middorsal blotches and smaller lateral blotches. In juveniles the venter is white with black transverse blotches; the chin is mostly black with white dots. In larger individuals the white venter changes to creamy yellow, and the black ventral markings change to dark gray or brown without greatly increasing in size; thus, adults appear to have paler venters than do juveniles. In juveniles the labials are gray with two or three vertical black bars; in adults the labials are uni-

formly yellowish tan. The terminal half of the tail is dull yellow above and below in small juveniles (< 455 mm total length) and yellow below in larger juveniles (< 470 mm total length). In adults the venter of the tail is darker in males than in females. ♂ 1024+181 mm; ♀ 1288+222 mm.

Occurrence.—*Bothrops atrox*, locally called *equis*, because of the X-shaped dorsal markings, is the most abundant pit viper in the area. Only two were found in primary forest, whereas 11 were in secondary forest, one at forest edge, and four in clearings. These account for only 18 of the 36 specimens; others were captured by natives, usually around their homes or in their cultivated clearings.

Eleven individuals were found on vegetation at night. Most of these were juveniles coiled on large leaves less than 1.5 m above the ground, but individuals having body lengths to 732 mm were

found in trees. One was crawling along a branch about 4 m above the ground, and another was coiled on a vine about 1 m above the ground. Individuals have been observed actively moving by day and night.

Life History.—A female collected in July (1073 mm in body length) contained 18 embryos, and one from November (1197 mm in body length) contained 24 embryos. Juveniles having body lengths of 227–340 mm were found in February (1), May (2), June (1), July (4), and August (1). These limited data suggest that the reproductive season is lengthy or most likely extends throughout the year.

Food.—Five juveniles contained food: two frogs, *Leptodactylus mystaceus*, and two lizards, *Ameiva ameiva petersii* and *Leposoma parietale*. These items indicate that *Bothrops atrox* probably feeds by night and day.

***Bothrops bilineatus smaragdinus* Hoge**

(FIGURE 164)

Material.—Santa Cecilia, 2.

Identification.—This distinctive, green pit viper has a prehensile tail and thereby differs from all other pit vipers in the area. The only other heavy-bodied, arboreal green snake in the area is the boa, *Corallus caninus*, which has smooth scales, sensory pits in the labials, and no sensory pit between nostril and eye.

The dorsum is pale green with minute black flecks; a pale yellow stripe occurs on the first row of dorsal scales. The edges of the ventrals are pale green, and the belly is white. The lips are yellowish green, and the iris is pale green. ♂ 365+64 mm; ♀ 555+90 mm.

Occurrence.—One male was crawling along a leafy vine 2 m above the ground in primary forest at night. The other specimen was brought in by a native. Apparently this snake, locally called *loro* (parrot), is more common than our few specimens indicate. At the time of our field work at Santa Cecilia in 1968 and



FIG. 164.—*Bothrops bilineatus smaragdinus*, ♂, 429 mm SVL (KU 112296).

1969, two trail cutters working for the oil company were bitten by *loros*.

Life History.—A female obtained in February contained immature ovarian eggs.

Bothrops castelnaudi

Duméril, Bibron and Duméril

Material.—Santa Cecilia, 1.

Identification.—This slender pit viper differs from other *Bothrops* in the area by its distinctive coloration. The dorsum is pale greenish gray with yellow flecks and square black blotches middorsally and smaller black spots laterally; the ventral surfaces are dark brown with pale yellow flecks, especially anteriorly. *Bothrops bilineatus* differs by being green with a yellow ventrolateral stripe, and *B. atrox* has a blotched black and white or brown and cream venter and no yellow flecks dorsally. *Lachesis muta* has dorsal scales in 35 rows (25 in *B. castelnaudi*), four or five rows of scales between the orbit and the labials (two rows in *B. castelnaudi*) and a tan dorsum with dark brown marks. The single specimen from Santa Cecilia is a female: 486+84 mm.

Occurrence.—The single specimen, obtained by a native, has no ecological data.

Life History.—No data are available.

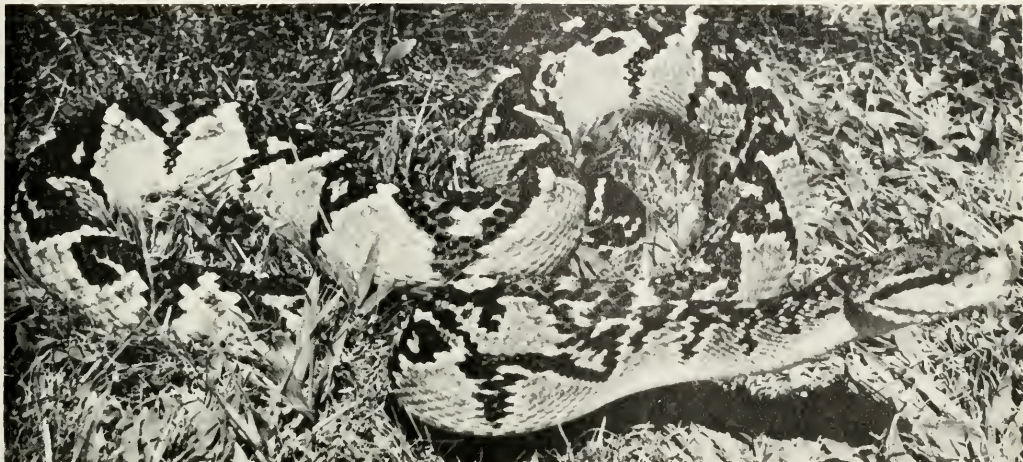


FIG. 165.—*Lachesis muta muta*, Santa Cecilia (Photo by Joseph T. Collins).

Lachesis muta muta (Linnaeus)

(FIGURE 165)

Material.—Santa Cecilia, 2.

Identification.—The largest pit viper in the area differs from other pit vipers there by having knob-like keels on the middorsal scales, dorsal scales in 35 rows, and four or five rows of scales separating the orbit from the labials. Pit vipers of the genus *Bothrops* have straight, even keels on the dorsal scales, which are in 25 rows, and two rows of scales between the orbit and the labials.

The body is a rich golden tan to pinkish tan with large dark brown or black, middorsal, diamond-shaped marks,

usually narrowly bordered by cream. Vertical dark bars extend from the lateral corners of the blotches nearly to the ventrals. The top of the head is brown; a black postorbital stripe extends to the angle of the jaw. The lips are tan, and the venter is cream. ♀ 2030+180 mm.

Occurrence.—The bushmaster apparently is uncommon in the area. One was on the ground in primary forest, and another was next to a log at the edge of the forest. Both were inactive when found by day.

Life History.—One female having a body length of 2030 mm obtained in August contained 13 oviducal eggs, each about 29 mm in length.

REPRODUCTIVE BIOLOGY

The continued existence of a species in a community is dependent upon successful reproduction by the adults and survival of the eggs and young to sexual maturity. My purpose here is to review the accumulated data on reproduction in the herpetofauna at Santa Cecilia with respect to annual reproductive patterns, fecundity, and reproductive strategies. A cursory review of data summarized by Turner (1962), Tinkle, Wilbur, and Tilley (1970), Fitch (1970), and Salthe and Mecham (1974) reveals the limited ex-

tent of our knowledge of reproduction in tropical amphibians and reptiles. By far the most informative study is that by Crump (1974) on frogs at Santa Cecilia.

The following analysis has four limitations: 1) The unevenness of sampling throughout the year precludes an accurate picture of annual reproductive patterns; thus, annual patterns are at least as broad as demonstrated by the data and in many cases probably much more so. 2) The data on caecilians, salamanders, turtles and crocodilians are too few

to be useful; accordingly, these groups (total of 15 species) have been excluded from the analysis, which therefore includes only frogs, lizards, and snakes. 3) Only the reproductive condition of females was studied; I have been concerned with fecundity and time of breeding, and I echo Fitch's (1970:6) statement: "When fecund females are present in the population there are usually males available to inseminate them." 4) The actual frequency of breeding of individuals is unknown; therefore, the data pertain only to populations, and inferences to individual cycles must be extrapolated.

ANNUAL REPRODUCTIVE PATTERNS

Most studies of reproduction in amphibians and reptiles have been conducted in seasonal environments, in which environmental cues, such as changes in temperature, photoperiod, or rainfall initiate breeding activity; in at least some species these changes can be correlated with hormonal activity and gonadal development, as well. In the essentially aseasonal environment of Santa Cecilia, we must search for other factors that influence patterns of reproduction. These factors may be intrinsic, such as a cycle that was established in the evolutionary history of a species in a seasonal environment prior to its invasion of a more equable environment, or differences in the time required for development of the ova. Extrinsic factors might include slight fluctuations in rainfall, prolonged periods of heavy cloud cover or many consecutive days of intense sunlight; moonlight has a distinctly negative effect on the activity of nocturnal species.

In the following discussion anurans, lizards, and snakes are treated separately prior to a final synthesis.

Anurans

The amount of data on each of the

87 species of frogs and toads is highly variable, but the aggregate is much more extensive than that for the lizards and snakes. Crump (1974) presented an account of 74 species from Santa Cecilia based on data that she accumulated in 1971-73. I have augmented her data with additional information from previous work at Santa Cecilia and the other study sites.

Three criteria must be clarified before discussing reproductive patterns in anurans. Mode of reproduction, as defined by Salthe and Duellman (1973), is a concept combining the site of development of the eggs with the mode of development; the latter is a complex of factors, including rate and duration of development, size and stage at hatching, and kind of parental care, if any. I recognize 11 modes of reproduction amongst the anurans at Santa Cecilia. Crump (1974) recognized 10 modes; she combined my modes 4 and 5 into one category. The reproductive modes are defined in Table 10. The ovarian size factor (Duellman and Crump, 1974) is an index for comparing fecundity and egg size relative to adult body size by means of the formula $CS(OD)/SVL$, where CS =clutch size, OD =ovum diameter, and SVL =snout-vent length of females depositing clutches. In the present study, mature ovarian complement was substituted for clutch size. I have followed Crump (1974) in distinguishing different types of annual reproductive patterns:

Continuous.—Gravid females and/or juveniles found throughout the year.

Opportunistic.—Species that breed regularly after heavy rains which occur throughout the year. Therefore, these species are somewhat more restricted in their breeding activity than are the continuous breeders.

Sporadic Wet.—Species that breed sporadically after heavy rains; these species breed less frequently than the opportunistic breeders.

TABLE 10.—Distribution of Reproductive Modes among Species of Anurans.

SITE OF DEVELOPMENT	Pipidae	Leptodactylidae	Bufo	Dendrobatidae	Hylidae	Centrolenidae	Ranidae	Microhylidae	Total
Eggs and larvae in water:									
A. <i>Mode 1</i> —unconstrained body of water		1	4		24		1	5	35
B. <i>Mode 2</i> —tree cavity above ground					1				1
C. <i>Mode 3</i> —constructed nest					1				1
Eggs out of water; larvae develop in water:									
D. <i>Mode 4</i> —eggs on vegetation above pond					11				11
E. <i>Mode 5</i> —eggs on vegetation above stream						3			3
F. <i>Mode 6</i> —eggs in foam nest; larvae in water		9							9
G. <i>Mode 7</i> —eggs on land; larvae carried to water				6					6
Neither eggs nor larvae unprotected in water:									
H. <i>Mode 8</i> —eggs and larvae in terrestrial nest		1							1
I. <i>Mode 9</i> —terrestrial eggs with direct development		17						1	18
J. <i>Mode 10</i> —eggs undergoing direct development on back of aquatic female	1								1
K. <i>Mode 11</i> —eggs undergoing direct development on back of terrestrial female					1				1

Sporadic Dry.—Species that breed sporadically during dry periods; these species breed least frequently of any of the anurans in the area.

The relationships between annual reproductive patterns and mode of reproduction are summarized in Table 11.

When viewing the entire anuran fauna, it is evident that reproduction occurs throughout the year (Fig. 166); examination of all female frogs collected reveals that the percentage of gravid females varies from 54 percent in July to 86 percent in February. However, when the data are examined with respect to species, we find no more than 49 (56% of total species) species gravid in a given month (July), when a total

of 64 species was found; thus, 77 percent of the species found in that month included gravid females. The extremes in the relative numbers of species to species gravid varies from 61 percent in August to 85 percent in February. It is interesting to note that in 1971-72, years when most of the data were accumulated, less rain fell in August and February than any other months (see Table 2).

When annual reproductive patterns are examined with respect to mode of reproduction (Table 11), we find only two unique combinations include more than one species. Thus, the centrolenids that deposit eggs on vegetation over streams (mode 5) breed sporadically after rains, and all species that carry

TABLE 11.—Anuran Annual Reproductive Patterns in Relation to Mode of Reproduction.
(Percentages in parentheses; see Table 10 for definitions of modes.)

MODE	Continuous	Opportunistic	Sporadic Wet	Sporadic Dry	TOTAL
1	8 (9.2)	8 (9.2)	19 (21.8)	-----	35 (40.2)
2	-----	-----	1 (1.1)	-----	1 (1.1)
3	-----	-----	-----	1 (1.1)	1 (1.1)
4	-----	5 (5.7)	6 (6.9)	-----	11 (12.2)
5	-----	-----	3 (3.4)	-----	3 (3.4)
6	1 (1.1)	1 (1.1)	4 (4.6)	3 (3.4)	9 (10.3)
7	6 (6.9)	-----	-----	-----	6 (6.9)
8	-----	-----	1 (1.1)	-----	1 (1.1)
9	10 (11.5)	-----	8 (9.2)	-----	18 (20.7)
10	1 (1.1)	-----	-----	-----	1 (1.1)
11	-----	-----	1 (1.1)	-----	1 (1.1)
TOTAL	26 (29.8)	14 (16.0)	43 (49.2)	4 (4.5)	87 (100)

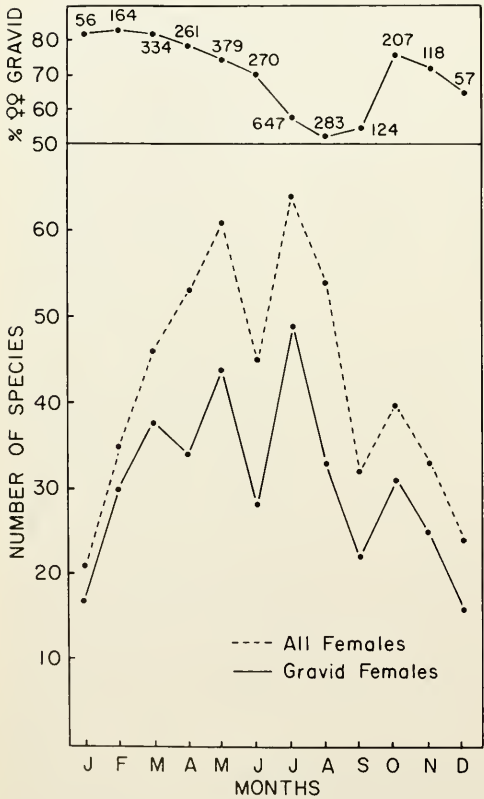


FIG. 166—Annual distribution of female frogs; upper graph is percent of gravid females (79 species); numbers above data points are total number of females.

their tadpoles from terrestrial ovipositional sites to water (dendrobatids) (mode 7) seem to be continuous breeders.

Nearly half of the species at Santa Cecilia are classified as sporadic, wet breeders; I suspect that further study will reveal that some of these are more opportunistic or actually continuous breeders. Many of the 18 species having terrestrial eggs with direct development (mode 9) are represented by few specimens; thus, more data probably would reveal that several of the species with mode 9 are continuous, rather than sporadic, wet breeders. Frogs having eight of the 11 recognized modes of reproduction are sporadic, wet breeders; only five modes are represented among the continuous breeders, accounting for 29.8 percent of the 87 species (Table 12).

Although the data are woefully incomplete for many species, on the basis of the presence of gravid females of at least some species in each month and the climatic equitability, it is reasonable to conclude that anurans at Santa Cecilia are capable of breeding throughout the year. Rainfall is probably the single most important environmental factor controlling time of breeding, the breeding activity of most species is positively

TABLE 12.—Monthly Distribution of Females with Mature Ovarian Eggs of Nine Common Species of Frogs.
(First line is number of females; second line is percent of females with mature ovarian eggs. See Table 10 for definition of modes.)

	MODE	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
<i>Dendrophryniscus minutus</i>	1	3 100	6 100	25 92	4 100	17 82	2 50	25 40	6 33	5 40	6 0	4 25	8 12	111 60
<i>Hyla alboguttata</i>	1	2 50	4 100	8 88	4 100	6 50	11 46	27 37	23 17	11 46	9 44	2 50	2 0	109 44
<i>Hyla rhodopepla</i>	1	2 100	2 100	16 100	5 100	7 86	23 95	28 89	1 0	1 0	20 90	15 100	5 100	125 92
<i>Hyla rubra</i>	1	3 100	7 100	12 92	2 100	10 100	13 100	24 87	0 0	5 60	14 86	16 75	0 0	106 88
<i>Leptodactylus mystaceus</i>	6	1 100	5 100	4 75	2 0	3 33	0 0	7 70	3 33	3 0	4 75	5 60	1 0	38 58
<i>Dendrobates parvulus</i>	7	4 100	15 100	27 89	11 88	29 89	25 89	31 94	7 86	3 100	11 88	8 100	2 100	115 90
<i>Eleutherodactylus croceoguinis</i>	9	7 100	8 100	15 93	21 100	22 95	7 100	18 67	6 67	2 50	6 100	1 100	2 100	115 89
<i>Eleutherodactylus lanthanites</i>	9	3 100	11 64	16 62	28 71	23 74	14 86	42 50	16 70	2 0	1 100	3 33	2 100	161 65
<i>Eleutherodactylus variabilis</i>	9	10 70	30 93	36 86	14 72	23 83	26 92	47 92	44 36	19 37	20 80	11 78	9 67	289 67
TOTAL FEMALES		35	88	159	85	140	121	249	106	51	91	65	31	1227
MEAN PERCENT GRAVID		91	95	86	81	76	73	64	36	37	74	69	54	71

correlated with increases in rainfall. Some species breed only after heavy rains that result in the ephemeral kinds of ponds that are utilized for their breeding. Because heavy rains are sporadic, the breeding patterns of such species, likewise, are sporadic. A few species breed at times of low rainfall, and these too are sporadic breeders.

Lizards

Despite a recent proliferation of information on reproduction in tropical lizards (for summaries, see Fitch, 1970; Tinkle, Wilbur, and Tilley, 1970; Sherbrooke, 1975; Simmons, 1975), knowledge of the reproductive biology of tropical species, particularly those in South America, is scanty. Only two of the 30 species at Santa Cecilia (*Ameiva ameiva* and *Neusticurus ecleopus*) have been studied in detail (Simmons, 1975; Sherbrooke, 1975).

The percentage of females of all species at Santa Cecilia that are gravid varies from 60 percent in January to 25 percent in December (Fig. 167). These months are represented by small samples; nonetheless, these extremes are closely approached by females from July and September, months having adequate sample sizes. The number of species that are gravid varies from one in January to 15 in July. Because only two species are represented from January, the data for that month probably have little significance, but in July 22 species are represented. Of the 596 adult female lizards, 274 (46%) contained mature ovarian or oviducal eggs.

Sherbrooke (1975:202) suggested that annual reproductive patterns in lizards might be classified as: 1) Continuous – without variation in reproductive activity; 2) Continuous with variation in reproductive activity – noted by seasonal variation either in testis size and/or spermatogenetic activity or percentage of females either fecund or ovigerous; or 3) Non-continuous – with periods when all individuals are reproductively inac-

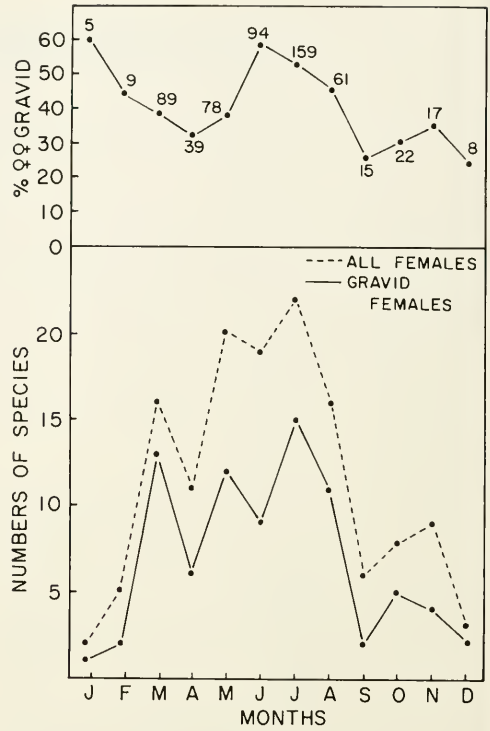


FIG. 167.—Annual distribution of female lizards; upper graph is percent of gravid females (30 species); numbers above data points are total number of females.

tive. The data on lizards at Santa Cecilia are incomplete. In fact, adequate data are available for only four species, three of which are *Anolis*, which evidently breed throughout the year (Fig. 168). The other species is *Ameiva ameiva*, females of which contained oviducal eggs from May through December (93 specimens). Simmons' (1975) analysis of ova size and volume of fat bodies demonstrated the cyclic reproductive pattern in this species.

By combining data from Santa Cecilia with those provided by Dixon and Soini (1975) for many of the same species at Iquitos, Perú (Fig. 169), it is possible to obtain a better idea of annual reproductive patterns in the lizards. Still, I am unable to demonstrate accurately the three patterns, as suggested by Sherbrooke (1975). With the present amount of data, the following 13 species

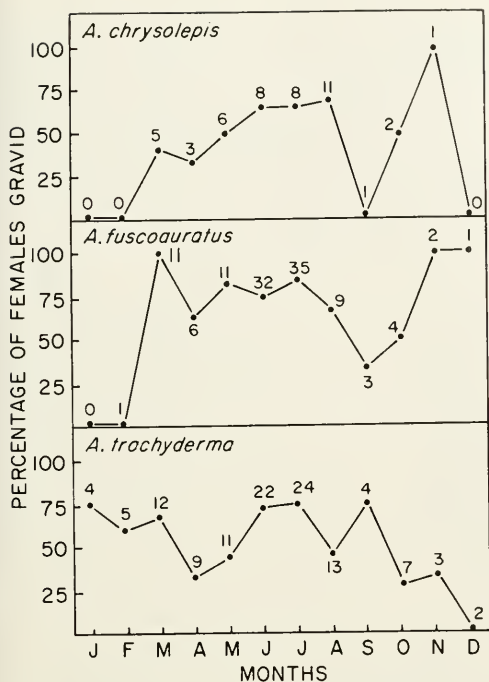


FIG. 168.—Percent of females gravid throughout the year in three species of *Anolis*: numbers above data points are total number of females.

seem to be continuous breeders: *Gonatodes concinnatus*, *Pseudogonatodes guianensis*, *Anolis* (all six species), *Plica umbra*, *Kentropyx elegans*, *Leposoma parietale*, *Neusticurus ecleopus*, and *Prionodactylus argulus*. The following seven species probably are non-continuous breeders: *Thecadactylus rapicauda*, *Enyaliodes cofanorum* and *laticeps*, *Alopoglossus atriventris* and *copei*, *Ameiva ameiva*, and *Mabuya mabouya*. Data are either non-existent or too meager for the other nine species to assign them to a category. Of the non-continuous breeders, the breeding season is longest in *Ameiva ameiva* (May-December), whereas females with oviducal eggs of the other species were found only in March-August.

Generally those species that are continuous breeders are small lizards; the range in mean snout-vent length of gravid females is 26.5-100.7 ($\bar{x}=57.4$)

mm. The snout-vent lengths of the non-continuous breeders are 47.7-114.6 ($\bar{x}=89.1$) mm.

Snakes

To one who has worked extensively in lowland tropical rainforests, it is soon obvious that snakes are not found in large numbers. The apparent scarcity of snakes becomes more obvious when the reproductive data are examined. Of 546 snakes from the Santa Cecilia area only 168 are adult females; only 26 (15.5%) of those were gravid (Fig. 170).

Examination of the data on those species best represented by females reveals no clear patterns (Table 13), and the paucity of data precludes any conclusions. The largest collection of snakes from any one area in the Amazon Basin is the Bassler Collection in the American Museum of Natural History; the snakes were collected over a period of several years in the region of Iquitos, Perú. Oliver (1947) reported on the *Leptophis ahuettulla* in the collection, and Fitch (1970) summarized the reproductive data on *Imantodes cenchoa*, *Leimadophis reginae*, *Leptodeira annulata*, *Xenodon severus*, and *Bothrops atrox*. They concluded that these six species (the only ones represented by adequate samples of gravid females and/or young) breed throughout the year. Perhaps the general trend in Amazonian snakes is to breed throughout most or all of the year, but I suspect that diverse patterns exist.

FECUNDITY

Although empirical data on frequency of reproduction are lacking for most of the species, it is possible to draw certain inferences from the quantitative assessments of ovarian complement, ova size, and female body size. This information provides some insight into the quantitative aspects of reproduction in the herpetofauna. The available data are much more substantive for the anurans than for the lizards; data are meager for snakes. I have drawn upon material

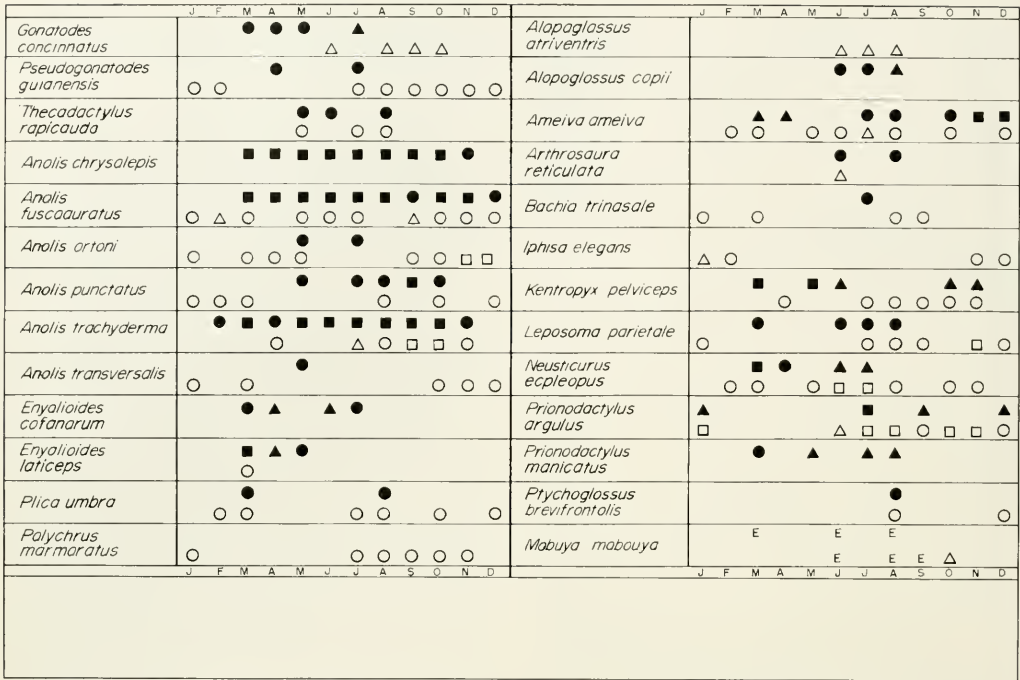


FIG. 169.—Reproductive data for 26 species of lizards from the Santa Cecilia region, Ecuador, compared with data from the Iquitos region, Perú (Dixon and Soini, 1975). Circles represent the presence of mature oviducal eggs; triangles represent hatchlings; squares represent eggs and hatchlings, and E's represent embryos. Solid symbols are data for Santa Cecilia; open symbols are data for Iquitos.

from other localities in the Amazon Basin and from the literature in order to have comparative data for some of the species of lizards and several species of snakes that are poorly represented in the collections from Santa Cecilia. As before, anurans, lizards, and snakes are discussed independently.

Anurans

Crump's (1974) thorough analysis of quantitative reproductive variables in 66 species at Santa Cecilia obviates any lengthy discussion of the data here. Her data base has been expanded to 76 species (Table 14). The additional data lend more support to Crump's conclusions regarding size-fecundity relationships; these conclusions can be summarized, as follows:

1. Species depositing eggs in water have larger ovarian complements (143-

8598, $\bar{x}$ =1225.3, N =31) than do those depositing eggs in aquatic foam nests (81-1589, $\bar{x}$ =457.0, N =6) or on vegetation over water (61-1036, $\bar{x}$ =342.5, N =11).

2. Species having terrestrial eggs undergoing direct development but no parental care have larger ovarian complements (5-62, $\bar{x}$ =19.3, N =17) than do those species in which the adults carry tadpoles (7-28, $\bar{x}$ =13.7, N =6).

3. Species depositing eggs in water have smaller eggs (0.8-2.1 mm, $\bar{x}$ =1.35, N =31) than those depositing eggs in a foam nest (1.0-2.4 mm, $\bar{x}$ =1.85, N =6) or on vegetation over water (1.0-3.6 mm, $\bar{x}$ =1.91, N =11).

4. Species having terrestrial eggs undergoing direct development have larger eggs (1.8-4.1 mm, $\bar{x}$ =2.72, N =17) than those having terrestrial eggs hatching into tadpoles (1.5-2.8 mm, $\bar{x}$ =1.88, N =6).

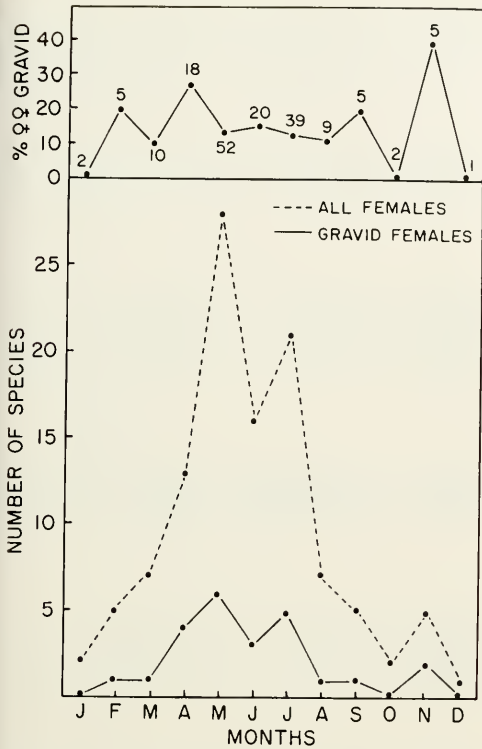


FIG. 170.—Annual distribution of female snakes; upper graph is percent gravid females (52 species); numbers above data points are total number of females.

5. The ovarian size factor is highest and most variable in species depositing eggs in water (4.9-110.2, $\bar{x}$ =24.7, N =31), followed by species depositing eggs on vegetation over water (4.5-26.2, $\bar{x}$ =8.9, N =11) and in foam nests (1.1-8.4,

$\bar{x}$ =4.2, N =6). Among species depositing eggs in water, the ovarian size factor is greater in larger species.

6. The ovarian size factor is lowest in those species having terrestrial eggs undergoing direct development (0.5-4.4, $\bar{x}$ =1.2, N =6).

7. In some species within a given reproductive mode there is a positive correlation between the number of eggs and the size of the female.

8. In some species within a given reproductive mode there is a positive correlation between ovum size and the size of the female.

Lizards

Size of females and reproductive mode (viviparous versus oviparous) are not highly correlated with the size of the ovarian complement in most lizards. Instead, the size of the ovarian complement seems to be rather constant within phylogenetic groups (Table 15). All gekkonids have only one oviducal egg at one time; anoles (Iguanidae) have one or two oviducal eggs, and microteiid normally have two eggs. Comparison of ovarian complement with size of female in the other lizards shows a positive correlation (Fig. 171).

Generally, the smaller species of lizards have smaller eggs; the length of oviducal eggs ranges from 5.2 mm in *Leposoma parietale* to 33.7 mm in *Tupi-*

TABLE 13.—Monthly Distribution of Females of Six Species of Snakes with Mature Eggs. (First line is number of females; second line is number of gravid females with mature eggs.)

	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
<i>Dipsas catesbyi</i>	0	0	0	4	2	1	3	0	1	0	0	0	11
	0	0	0	2	0	1	0	0	0	0	0	0	3
<i>Imantodes cenchoa</i>	1	0	2	0	2	1	1	1	0	0	1	0	9
	0	0	1	0	0	1	1	0	0	0	1	0	4
<i>Leimadophis reginae</i>	0	1	0	1	1	0	2	0	0	0	0	0	5
	0	1	0	1	0	0	0	0	0	0	0	0	2
<i>Leptophis ahuetulla</i>	0	0	0	1	1	1	1	0	0	0	0	0	4
	0	0	0	1	0	0	1	0	0	0	0	0	2
<i>Oxybelis argenteus</i>	1	1	2	1	1	1	4	3	1	0	1	0	16
	0	0	0	0	0	0	1	1	0	0	0	0	2
<i>Bothrops atrox</i>	0	1	2	1	2	1	3	0	1	0	1	0	12
	0	0	0	0	0	0	1	0	0	0	1	0	2

TABLE 14.—Size-Fecundity Relationships of Anurans Based on Mature Ovarian Complement.
(See text for definition of reproductive modes and patterns; a dagger indicates tentative assignments to mode or pattern.)

SPECIES	MODE	Pattern	N	♀ Snout-vent Length		Ovarian Complement		Max. Ovary Diameter	Ovarian Size Factor
				Mean	Range	Mean	Range		
<i>Ceratophrys cornuta</i>	1	W†	1	101.0	—	1750.0	—	1.9	32.0
<i>Bufo glaberrimus</i>	1	W†	—	—	—	—	—	—	—
<i>Bufo marinus</i>	1	W	5	132.6	115-146	8598.0	4240-12700	1.7	110.2
<i>Bufo typhlonius</i>	1	C	14	73.8	54-87	1537.8	310-2500	1.8	37.5
<i>Dendrophryniscus minutus</i>	1	C	41	19.1	17-22	150.6	70-245	0.9	7.1
<i>Hyla alboguttata</i>	1	C	21	41.4	35-46	440.1	210-870	1.4	14.9
<i>Hyla calcarata</i>	1	W	10	53.9	47-61	1143.5	835-1600	1.6	33.9
<i>Hyla cruentomma</i>	1	W	18	28.3	25-32	580.4	280-1200	1.1	22.6
<i>Hyla fasciata</i>	1	C	27	47.3	45-51	569.1	360-870	1.5	18.1
<i>Hyla funera</i>	1	W	13	37.9	33-43	537.8	225-740	1.1	15.6
<i>Hyla garbei</i>	1	C	21	41.9	39-48	550.8	280-793	1.5	19.7
<i>Hyla geographica</i>	1	W	7	66.6	64-69	2797.1	1780-4300	1.2	50.4
<i>Hyla granosa</i>	1	W	11	41.2	40-44	426.4	350-520	1.5	15.5
<i>Hyla lanciformis</i>	1	C	23	87.3	79-94	1617.5	740-2400	2.0	37.1
<i>Hyla marmorata</i>	1	O	10	49.3	46-53	1145.8	740-1580	1.3	30.2
<i>Hyla minuta</i>	1	W	5	23.8	23-24	211.6	160-265	1.0	8.9
<i>Hyla parviceps</i>	1	C	101	23.3	20-26	234.1	120-395	1.1	9.1
<i>Hyla punctata</i>	1	W	20	37.2	35-41	324.6	230-430	1.5	13.1
<i>Hyla rhodopepla</i>	1	O	52	26.8	23-28	285.4	140-422	1.1	11.7
<i>Hyla riveroi</i>	1	W†	—	—	—	—	—	—	—
<i>Hyla rossalleni</i>	1†	W†	—	—	—	—	—	—	—
<i>Hyla rubra</i>	1	O	66	39.5	35-44	521.4	68-960	1.5	19.8
<i>Osteocephalus buckleyi</i>	1	O†	1	49.0	—	580.0	—	1.2	14.2
<i>Osteocephalus lepreurii</i>	1	O	16	59.8	56-64	848.1	480-1150	1.2	17.0
<i>Osteocephalus taurinus</i>	1	O	1	76.0	—	550.0	—	1.0	7.2
<i>Phrynohyas coriacea</i>	1	O†	1	66.0	—	1430.0	—	1.9	41.2
<i>Phrynohyas venulosa</i>	1	O	—	—	—	—	—	—	—
<i>Sphaenorhynchus carneus</i>	1	W†	1	23.0	—	143.0	—	1.2	7.5
<i>Sphaenorhynchus eurhustus</i>	1	W†	1	48.0	—	550.0	111	1.2	13.8
<i>Rana palatipes</i>	1	C	25	116.9	103-126	2859.8	720-6750	2.0	49.4
<i>Chiasmocleis anatipes</i>	1	W	—	—	—	—	—	—	—
<i>Chiasmocleis basleri</i>	1	W	3	27.3	25-30	212.0	151-250	1.2	9.3
<i>Chiasmocleis ventrimaculata</i>	1	W	1	22.0	—	210.0	—	0.8	7.6
<i>Ctenophryne geayi</i>	1	W	1	54.0	—	1250.0	—	1.3	30.1
<i>Hamptophryne boliviana</i>	1	W	2	42.0	40-44	1778.0	1370-2186	1.2	50.8
<i>Nyctimantis rugiceps</i>	2	W	1	63.0	—	773.0	—	1.3	16.0

TABLE 14.—Continued.

SPECIES	MODE	Pattern	N	♀ Snout-vent Length		Ovarian Complement		Max. Ovary Diameter	Ovarian Size Factor
				Mean	Range	Mean	Range		
<i>Hyla boans</i>	3	D	25	99.0	80-110	3154.8	1300-1800	2.1	66.9
<i>Hyla bifurca</i>	4	O	20	32.9	29-35	190.0	145-255	1.5	8.7
<i>Hyla bokermanni</i>	4	O	29	23.9	23-26	98.3	65-135	1.3	5.3
<i>Hyla brevifrons</i>	4	O	15	20.9	18-24	79.1	48-114	1.1	4.2
<i>Hyla favosa</i>	4†	W†	1	40.0	—	496.0	—	1.0	12.4
<i>Hyla leucophyllata</i>	4	W	12	42.1	40-44	572.3	220-928	1.3	17.7
<i>Hyla sarayacuensis</i>	4	O	14	33.6	31-37	113.4	68-176	2.0	6.8
<i>Hyla triangulum</i>	4	O	23	39.5	36-42	501.7	320-650	1.5	19.1
<i>Phyllomedusa palliata</i>	4	W	15	46.5	44-49	60.8	38-106	2.6	3.4
<i>Phyllomedusa tarsius</i>	4	W	15	105.3	95-111	548.7	410-750	3.1	16.2
<i>Phyllomedusa tomonterna</i>	4	W	5	57.2	55-60	71.4	60-89	3.6	4.5
<i>Phyllomedusa vaillanti</i>	4	W	6	78.8	68-84	1036.2	645-1250	2.0	26.3
<i>Centrolenella midas</i>	5	W	4	25.5	23-28	22.0	14-29	1.5	1.3
<i>Centrolenella munozorum</i>	5	W	1	23.0	—	18.0	—	1.5	1.2
<i>Centrolenella resplendens</i>	5	W†	—	—	—	—	—	—	—
<i>Edalorhina perezi</i>	6†	W†	2	37.0	36-38	81.0	69-98	2.0	4.4
<i>Leptodactylus discodactylus</i>	6†	W	5	33.6	33-35	234.8	148-420	1.2	8.4
<i>Leptodactylus mystaceus</i>	6	C	22	54.8	52-60	280.5	171-425	2.4	1.2
<i>Leptodactylus pentadactylus</i>	6	D	—	—	—	—	—	—	—
<i>Leptodactylus rhodomystax</i>	6	D†	—	—	—	—	—	—	—
<i>Leptodactylus stenodema</i>	6	D†	—	—	—	—	—	—	—
<i>Leptodactylus wagneri</i>	6	W	7	67.3	51-77	1588.6	1000-3150	1.5	2.0
<i>Lithodytes lineatus</i>	6†	W†	2	53.5	51-56	212.5	195-230	2.0	7.9
<i>Physalaemus petersi</i>	6	O†	1	32.0	—	340.0	—	1.0	1.1
<i>Colostethus marchesianus</i>	7	C	40	17.8	16-19	14.0	7-27	1.5	1.2
<i>Colostethus sauli</i>	7	C	6	25.0	24-26	11.3	6-14	1.5	0.7
<i>Dendrobates parvulus</i>	7	C	109	21.0	18-23	8.9	4-16	2.8	1.2
<i>Dendrobates pictus</i>	7	C	48	22.5	20-24	18.0	6-31	2.1	1.7
<i>Dendrobates quinquevittatus</i>	7	C†	2	16.0	16	6.5	4-9	1.5	0.6
<i>Phyllobates femoralis</i>	7	C	12	25.6	24-28	22.7	8-43	1.9	1.7
<i>Adenomera andreae</i>	8	W†	12	26.7	25-29	8.7	6-16	3.0	1.0
<i>Eleutherodactylus acuminatus</i>	9	W†	6	28.8	27-31	17.2	12-21	2.4	1.4
<i>Eleutherodactylus altamazonicus</i>	9	C	20	28.1	27-32	18.2	12-25	2.5	1.6
<i>Eleutherodactylus conspicillatus</i>	9	C	10	42.3	40-45	42.8	27-62	3.5	3.5
<i>Eleutherodactylus croceinguinis</i>	9	C	86	20.3	18-23	4.8	2-7	2.8	0.7
<i>Eleutherodactylus diadematus</i>	9	W†	5	42.4	40-45	61.6	43-108	3.0	4.4

TABLE 14.—Concluded.

SPECIES	MODE	Pattern	N	♀ Snout-vent Length		Ovarian Complement		Max. Ovary Diameter	Ovarian Size Factor
				Mean	Range	Mean	Range		
<i>Eleutherodactylus lacrimosus</i>	9	C	11	23.5	20-29	9.5	7-16	2.5	1.0
<i>Eleutherodactylus lantianites</i>	9	C	68	38.7	34-46	30.4	20-52	3.2	2.5
<i>Eleutherodactylus martiae</i>	9	C	18	21.7	19-23	7.8	5-13	2.0	0.7
<i>Eleutherodactylus nigrovittatus</i>	9	C†	3	22.0	22	9.3	9-10	2.5	1.1
<i>Eleutherodactylus ockendeni</i>	9	C	29	26.4	23-29	13.0	5-18	2.8	1.4
<i>Eleutherodactylus orphnolaimus</i>	9	W†	1	19.0	---	5.0	---	2.0	0.5
<i>Eleutherodactylus paululus</i>	9	W†	12	20.8	18-22	7.3	4-11	3.0	1.1
<i>Eleutherodactylus pseudocaminatus</i>	9	W†	1	29.0	---	22.0	22	2.6	2.0
<i>Eleutherodactylus quaquavertus</i>	9	W†	1	49.0	---	32.0	---	2.5	1.6
<i>Eleutherodactylus sulcatus</i>	9	W†	148	24.4	22-29	6.7	2-11	3.0	0.8
<i>Eleutherodactylus variabilis</i>	9	C	34	52.9	47-62	35.1	15-51	4.1	2.7
<i>Ischnocnema quixensis</i>	9†	W†	5	13.4	12-14	5.4	5-6	1.8	0.7
<i>Syncope antenori</i>	10	C†	1	67.0	---	26.0	---	---	---
<i>Pipa pipa</i>	11	W†	1	---	---	---	---	2.5	1.0
<i>Hemiphractus proboscideus</i>	---	---	---	---	---	---	---	---	---

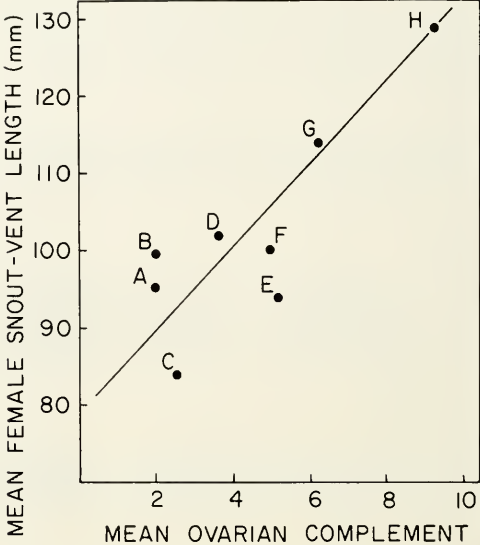


FIG. 171.—Mean size-fecundity relationships in eight species of lizards: A. *Uracentron flaviceps*, B. *Enyaliodes cofanorum*, C. *Plica umbra*, D. *Ameiva ameiva*, E. *Mabuya mabouya*, F. *Kentropyx pelviceps*, G. *Enyaliodes laticeps*, H. *Polychrus marmoratus*, $r=0.78444$; $P<0.05$.

nambis tequixin. However, if all lizards are considered there is no significant correlation between ovum length and female snout-vent length ($r=0.58028$; $P=>0.05$).

Presumably the gekkonids (with the possible exception of *Thecadactylus*), the anoles, and the microteiids (with the exception of the two species of *Alopoglossus*) have multiple broods. This assumption is based on the small clutch size (one or two eggs) and the presence of numerous gravid females throughout the year. *Plica umbra* and *Kentropyx pelviceps* appear to be continuous breeders and may have multiple clutches in a year. *Ameiva ameiva* is a cyclic breeder, and Simmons (1975) found no evidence for multiple broods. Limited data for other species suggest that single broods may be the rule in *Enyaliodes* and *Mabuya*.

Snakes

The paucity of data precludes any broad conclusions regarding fecundity; the meager data from Santa Cecilia have

TABLE 15.—Size-Fecundity Relationships of Lizards and Amphisbaenians Based on Mature Ovarian Complement.

SPECIES	N	♀ Snout-vent Length		Ovarian Complement		Mean Ovum Length
		Mean	Range	Mean	Range	
<i>Gonatodes concinnatus</i>	6	41.6	35–48	1.0		8.9
<i>Pseudogonatodes guianensis</i>	2	26.5	26–27	1.0		6.0
<i>Thecadactylus rapicauda</i>	4	107.8	97–116	1.0		19.0
<i>Anolis chrysolepis</i>	25	73.7	66–86	1.3	1–2	16.3
<i>Anolis fuscoauratus</i>	89	43.8	38–50	1.3	1–2	9.1
<i>Anolis ortonii</i>	4	42.5	42–43	1.5	1–2	9.9
<i>Anolis punctatus</i>	5	70.6	67–72	1.4	1–2	16.3
<i>Anolis trachyderma</i>	68	50.9	45–56	1.1	1–2	13.1
<i>Anolis transversalis</i>	1	72.0		1.0		14.4
<i>Enyaliodes confanorum</i>	2	99.5	92–107	2.0		27.4
<i>Enyaliodes laticeps</i>	5	114.6	107–125	6.3	5–7	15.8
<i>Plica umbra</i>	4	83.5	80–90	2.5	2–4	22.6
<i>Polychrus marmoratus</i> ^a	7	128.0	109–147	9.3	7–11	13.1
<i>Uracentron flaviceps</i> ^a	3	95.0	79–117	2.0		23.7
<i>Mabuya mabouya</i>	6	93.7	89–100	5.2	4–6	 ^b
<i>Alopoglossus atriventris</i> ^a	7	47.7	41–51	2.0		10.7
<i>Alopoglossus copii</i>	4	58.3	53–62	2.0		10.5
<i>Ameiva ameiva</i>	12	102.2	90–118	3.7	2–6	21.0
<i>Arthrosaura reticulata</i>	3	66.6	64–70	2.0		13.3
<i>Bachia trinasale</i>	2	74.5	70–79	2.0		11.0
<i>Dracaena guianensis</i>						
<i>Iphisa elegans</i>	1	52.0		2.0		7.6
<i>Kentropyx pelviceps</i>	3	100.7	95–106	5.0	4–6	17.5
<i>Leposoma parietale</i>	12	36.2	34–39	2.0		5.2
<i>Neusticurus ecleopus</i>	2	61.5	56–67	2.0		11.0
<i>Prionodactylus argulus</i>	4	42.5	39–44	1.8	1–2	9.1
<i>Prionodactylus manicatus</i>	1	64.0		2.0		15.0
<i>Ptychoglossus brevifrontalis</i>	2	58.5	58–59	2.0		8.3
<i>Tupinambis tequixín</i>	1	307.0		3.0		33.7
<i>Amphisbaena fuliginosa</i>						

^a Data from Dixon and Soini (1975).^b Viviparous.

been supplemented by additional data from specimens from other localities and from the literature (Table 16). Viviparous species, which also are among the larger snakes, have larger broods than do oviparous species. Mean ovarian complements of viviparous species are 10.42 ($\bar{x}$ =25.2, N =4) as compared to 1.8–22 ($\bar{x}$ =7.6, N =28) in oviparous species. Among the oviparous species, the largest ovarian complements were found in the larger heavy-bodied snakes, such as *Clelia*, *Oxyrhopus formosus*, *Xenodon*, and *Lachesis*. Moderately large complements (11–12) were found in the two aquatic *Helicops*, which may be facultatively viviparous (Rossman,

1973). The slender arboreal snakes (*Dipsas*, *Imantodes*, *Leptodeira*, *Leptophis*, and *Oxybelis*) have no more than six eggs.

There is no evidence from the data from Santa Cecilia that any of the snakes have multiple broods during the year. In fact, the presence of so few gravid females suggests that reproduction within individuals may be cyclic – perhaps annual or bi-annual. On the other hand, some of the more abundant species, such as *Oxybelis* and *Leptodeira*, have smaller clutches than do less common species, such as *Boa*, *Clelia*, and *Xenodon*. If the limited data on clutch sizes and relative abundance have any significance,

TABLE 16.—*Concluded.*

SPECIES	MODE	N	♀ Snout-vent Length		Ovarian Complement		Mean Ovum Length	Source
			Mean	Range	Mean	Range		
<i>Oxyrhopus petola</i>	O	1	761	---	4.0	---	34.2	
<i>Pseudoboa coronata</i>	O			---		---		
<i>Pseustes sulphureus</i>	O			---	2.0	---	26.2	
<i>Rhadinaea brevirostris</i>	O	1	269	---		---		
<i>Siphlophis cervinus</i>	O			---		---		
<i>Tantilla melanocephala</i>	O			---		---		
<i>Tripanurgos compressus</i>	O			---		---		
<i>Xenodon severus</i>	O	1	1060	---	2.0	---		
<i>Xenopholis scalaris</i>	O	1	317	---	3.0	---	23.9	
<i>Leptomicrurus narducci</i>	O			---		---		
<i>Micrurus langsdorffi</i>	O			---		---		
<i>Micrurus lemniscatus</i>	O			---		---		
<i>Micrurus spixii</i>	O			---		---		
<i>Micrurus surinamensis</i>	O	1		---	11.0	---	40.0	Schmidt (1951:31)
<i>Bothrops atrox</i>	V	2	1135	1073-1197	21.0	18-24		
<i>Bothrops bilineatus</i>	V			---		---		
<i>Bothrops castelnaudi</i>	V			---		---		
<i>Lachesis muta</i>	O	1	2013	---	13.0	---	29.0	

perhaps the more abundant species with small clutches have multiple broods annually.

REPRODUCTIVE STRATEGIES

Reproductive strategies are as significant to the survival of a species as are physiological and morphological adaptations to the environment. As pointed out as early as 1930 by Fisher, there must be differential selection on the utilization of resources towards reproduction. General theoretical approaches to the evolution of reproductive strategies have been advanced by Cole (1954), Williams (1966), and Gadgil and Bossert (1970). MacArthur and Wilson (1967) crystalized much of the earlier thinking with the concept of "*r*-selection and *K*-selection," in which reproductive potential is viewed with respect to the maximal intrinsic rate of natural increase (*r*-selection) and the carrying capacity of the environment (*K*-selection). Pianka (1970) emphasized that a continuum exists between *r*-selection and *k*-selection. Wilbur, Tinkle, and Collins (1974) provided a thoughtful reappraisal of *r*- and *K*-selection with respect to the evolution of life histories; they pointed out the necessity of considering ecological dimensions other than fecundity, such as trophic level and environmental predictability in gaining an understanding of the evolution of reproductive strategies.

Wilbur, Tinkle, and Collins (1974) enumerated the following components of a life history strategy and noted that each would be modified by natural selection so as to produce a strategy resulting in the highest individual fitness and reflecting a compromise among many selective pressures:

1. Juvenile and adult mortality schedules.
2. Age at first reproduction.
3. Reproductive life-span.
4. Fecundity (number and size of eggs, frequency of deposition, and

- proportion of females breeding).
5. Fecundity - age regression.
6. Degree of parental care.
7. Reproductive effort.

In discussing the reproductive strategies of the anurans and squamates at Santa Cecilia, emphasis is placed on fecundity with respect to environmental predictability and trophic level; degree of parental care is also considered, and some inferences can be made regarding reproductive effort. The data base necessary for complete coverage of the components listed above is entirely lacking for numbers 1, 2, 3, and 5, although some reasonable assumptions can be made about juvenile mortality and age at first reproduction. As in the foregoing discussions, anurans, lizards, and snakes are treated separately, and as before, the largest data base pertains to the anurans.

Anurans

A variety of reproductive modes have evolved in anurans (see Salthe and Duellman, 1973, and Crump, 1974, for recent discussions). It must be realized that these diverse reproductive modes are genetically fixed and do impose constraints on the species. Because these reproductive modes are important to understanding the reproductive strategies, the first part of the discussion is organized by the 11 reproductive modes occurring in anurans at Santa Cecilia. Other distinctive modes occur in frogs elsewhere, but because they are irrelevant to the anuran community under consideration, they are excluded.

Mode 1.—Eggs are deposited in unconstrained bodies of water, and tadpoles develop in the water (lotic or lentic; permanent or ephemeral). Clutches are large; eggs and hatchlings are small. Eggs and larvae in ephemeral ponds are subject to mortality due to desiccation of habitat. Eggs and larvae in all aquatic situations, especially large permanent bodies of water, are subject to predation by aquatic insects, snakes, birds, and

fish. Food probably is not a limiting resource except under conditions of habitat shrinkage and consequent crowding; most tadpoles are pelagic filter feeders, grazers, and bottom detritus-feeders, but some are carnivores. The generalized anuran reproductive mode is the most common mode at Santa Cecilia, occurring in 35 species in five families.

Mode 2.—Eggs and larvae develop in a water-filled cavity in a tree. Clutches are moderate-sized; eggs and hatchlings are small. Eggs and larvae likely are subject to mortality due to insufficient oxygen and to organic substances resulting from decay. Food is a limited resource; in at least one species (*Anothea spinosa*) not occurring at Santa Cecilia, the small tadpoles feed on insect larvae, and the larger tadpoles eat frog eggs, presumably those of their own species. This mode involves some behavioral and physiological modifications in the larvae from the generalized Mode 1. At Santa Cecilia this mode occurs only in the hyloid *Nyctimantis rugiceps*.

Mode 3.—Eggs are deposited in a basin-like nest constructed by the male or in a natural basin at the edge of a river. The tadpoles undergo at least their early development in the nest. Clutches are large, and the eggs and hatchlings are small. Any significant rise or fall of the level of the river next to the nest can result in either the flooding or desiccation of the nest. Predation by aquatic organisms probably is minimal, but the tadpoles in a constrained nest are easy prey for birds. The tadpoles are grazers; food certainly is a limited resource until the nest is flooded. Tadpoles usually are flushed from the nest before they complete their development; because they are not well-adapted for survival in lotic environments their early development in the nest enhances their survival in the flowing water. Also, developmental time should be reduced due to the warmer water in the shallow basin. This mode involves principally a behavioral adaptation on the part of the male

and the expenditure of energy in the construction of the nest. Nest-building at Santa Cecilia is practiced only by *Hyla boans*.

Mode 4.—Eggs are deposited on vegetation above lentic water. The clutches are moderately small, and the eggs are only slightly larger, if any, than those deposited in water. Small hatchlings drop into the water and complete their development. The eggs are freed from aquatic predators but are subjected to some terrestrial predators (dipteran larvae and one snake — *Leptodeira annulata*). The tadpoles are faced with the same environmental pressures as those in Mode 1. This mode is characteristic of frogs of the hyloid genus *Phyllomedusa* and also occurs in seven species of *Hyla* — a total of 11 species at Santa Cecilia.

Mode 5.—Eggs are deposited on vegetation above lotic water; hatchling tadpoles drop into the stream. Clutches are small, and eggs and hatchlings are moderately large. This mode is the same as Mode 4, except for the larger, muscular tadpoles with low fins; the tadpoles are well adapted for survival in torrential streams and actually spend most of their time under cover on the bottoms of streams. At Santa Cecilia this mode occurs only in the three species of *Centrolenella*.

Mode 6.—The eggs are suspended in a foam nest formed of air, water mucus, and semen by kicking action of the male during oviposition in ponds. The clutches are moderately large, and the eggs and hatchlings are small. The nest provides a moist environment for the development of the eggs and young tadpoles. Foam nests apparently are an adaptation to ephemeral aquatic habitats. Temporary desiccation of a pond will not adversely affect the nests, which develop a semipervious outer coating while maintaining a moist interior. Once the tadpoles enter the pond they are subject to the same environmental pressures as those in Mode 1. The principal modification in this mode is the behavior of

the male in kicking the gelatinous material around the fertilized eggs into a froth. Among Neotropical frogs, foam nests are constructed only by leptodactylines, of which nine species occur at Santa Cecilia.

Mode 7.—Eggs are deposited in secluded, moist places on the forest floor; upon hatching, the tadpoles are carried to water on the back of an adult frog. Clutches are small, and eggs and hatchlings are relatively large. This mode is characteristic of the family Dendrobatidae, represented at Santa Cecilia by six species in three genera. The tadpoles of *Phyllobates* and *Colostethus* are transported to small rivulets, where the tadpoles develop in quiet pools. The tadpoles of *Dendrobates* are transported to some constrained body of water in a tree stump, cavity in a log, base of a palm frond, or even some unnatural container, such as a tin can. Those tadpoles developing in rivulets are subjected to aquatic predators but probably have an abundance of food. The tadpoles of *Dendrobates* probably are confronted with fewer aquatic predators but possibly are limited by food; these tadpoles are cannibalistic, and frequently, only the one or two largest individuals in a given clutch will survive to metamorphosis. The behavioral modifications in dendrobatids involve not only the transportation of tadpoles (usually, but not always, by males) but also territoriality and a unique method of mating not involving amplexus (Goodman, 1971; Crump, 1972).

Mode 8.—Eggs are deposited in a foam nest like that of Mode 6, except that the nest is in a depression under a log or rock on land and the tadpoles undergo their entire development within the foam nest. Clutches are moderately small, and the eggs are relatively large. Hatchling tadpoles have a large yolk sac which provides the nutrients sufficient for the completion of development. Although the exigencies of the aquatic environment have been bypassed, the nest

is subject to desiccation and predation by terrestrial arthropods. This mode is merely a final step towards terrestriality in leptodactyline frogs and occurs in one species, *Adenomera andreae*, at Santa Cecilia.

Mode 9.—Eggs are deposited in secluded, moist, terrestrial or arboreal situations and undergo development direct into small frogs. Clutches are small, and eggs are large, containing sufficient yolk for the nutrition of the developing frog. Eggs are deposited amidst leaf litter, in and under logs, under stones, amidst moss, and in bromeliads. As in Mode 8, the environmental pressures of the aquatic environment have been circumvented. Although at least some species guard their eggs, the eggs are subject to desiccation and predation by arthropods, of which spiders and tenebrionid beetles are not infrequent. Upon hatching the young are already in the same environment as the adults and probably have an abundance of shelter and food. This mode is widespread world-wide in many families. At Santa Cecilia it occurs in 17 species of eleutherodactyline leptodactylids and presumably in one microhylid, *Synecope*.

Mode 10.—Eggs are deposited on the back of the female of an aquatic species; the eggs become covered with skin and undergo direct development into froglets, which emerge from their individual pouches and swim away. Clutches are moderately small, and the eggs are large. The most distinctive modification is the aerobic behavior involved in getting the egg from the cloaca to the back of the female (Rabb and Rabb, 1960). Also, there are histological modifications in the dorsal skin. Although this frog is strictly aquatic, the precarious aquatic egg and tadpole stages have been eliminated, and the development is completely under parental care. This mode occurs only in *Pipa pipa*.

Mode 11.—Eggs are carried on the back of a terrestrial female. Clutches are small, and eggs are large. The eggs

adhere to individual shallow depressions in the dorsal skin. The hatchlings have external gills which adhere to the female and attach to the young by a pair of cords. The parental care thereby given to the eggs and young provides at least partial avoidance of environmental stresses and predation. Thus, frogs having this mode have eliminated the major environmental pressures affecting eggs in Mode 9. This mode occurs in amphignathodontine and hemiphractine hylids represented at Santa Cecilia solely by *Hemiphractus proboscideus*.

Assuming that the habit of depositing eggs in permanent water is the primitive, as well as the generalized mode of reproduction in anurans, we can view other reproductive modes as adaptive strategies in response to diverse selective pressures resulting from changing environments or invasion of new environments. Permanent bodies of lentic water are localized, rare, or nonexistent in some areas of the world inhabited by frogs. Lotic habitats are more widespread but require certain modifications in oviposition and in the larvae for survival. Because stream-breeding frogs, in the strict sense, are absent at Santa Cecilia, they are not considered here.

The dispersal of pond-breeding frogs is greatly enhanced if they are capable of breeding in ephemeral aquatic habitats. In the upper Amazon Basin such habitats vary from shallow depressions that contain water only after heavy rains to forest pools that may fluctuate greatly in size and may dry up only for a few weeks during the year. The larger predatory fish characteristic of permanent water are absent from most of the ephemeral ponds, but small fish and predatory aquatic insects are present. Although frogs that breed in ephemeral ponds avoid some kinds of predators and increase the number of available breeding sites, they do face the problem of possible desiccation of the eggs and tadpoles. The adaptive response adopted by most of these frogs involves multiple

small clutches of small eggs undergoing rapid development into small young. In this way their entire reproductive energy is not put into a single large clutch, which may desiccate. Survival of the eggs and tadpoles is enhanced by depositing small clutches sporadically after heavy rains; the small eggs and larvae are in the water for only a short period of time.

The strategies of depositing eggs in constrained aquatic situations, either natural or constructed apparently are different in the two frogs that exhibit this behavior at Santa Cecilia. The ovarian size factor in *Nyctimantis rugiceps* is intermediate between that found in pond-breeding hylids and pouch-brooding hylids and may represent an intermediate evolutionary stage (Duellman and Trueb, 1976). The nest-building habit of *Hyla boans* seems to be associated with complex intraspecific territoriality, which presently is not understood.

Those species that deposit their eggs on vegetation above water exhibit another response for partially escaping the exigencies of aquatic environments. Although the eggs are not subject to aquatic predators and desiccation of the pond, they do fall prey to some terrestrial predators, and may desiccate. These frogs are like most that breed in ephemeral ponds in having multiple small clutches. However, many of them have larger eggs resulting in more advanced hatchlings, a way of abbreviating the dependency on the aquatic environment. In the case of those species depositing eggs over streams, the advanced larva is better able to survive in fast-flowing water than a small tadpole with a bulging yolk sac.

The construction of foam nests is a response involving behavioral adaptations of the frogs and an increase in the expenditure of energy by the males. Although the eggs are generally small, they are not so numerous as in those species depositing eggs in ponds. The

completion of development of tadpoles in terrestrial foam nests is an obvious escape from the aquatic environment, yet the nest itself is a quasi-aquatic situation.

The reproductive mode of depositing eggs on land and carrying the tadpoles to water (characteristic of all dendrobatids) involves complex territorial behavior and parental care. These traits will result in higher survivorship of the young, but with concomitant reduction in clutch size. At least at Santa Cecilia the dendrobatids appear to breed continuously, or nearly so.

The complete escape from the aquatic environment is exemplified by those species having terrestrial eggs undergoing direct development into small frogs. Parental care may, or may not, be involved. In order to provide sufficient nourishment for the entire development of the embryos, the eggs contain large quantities of yolk. The increased size of the eggs necessitates a decrease in clutch size. However, the reduced fecundity presumably is balanced by increased survivorship. The habit of carrying the eggs on the back of the female in a terrestrial environment adds another dimension of parental care. Except in cases of catastrophes involving the brooding females, survivorship of the eggs possibly is close to 100 percent.

The diverse reproductive strategies in this tropical anuran community are alternative means for effective reproduction. A simplistic approach would categorize those highly fecund species having reproductive Mode 1 as "r-strategists" and those species having reproductive Modes 7-10 (all low fecundity) as "K-strategists." Species exhibiting other modes and generally intermediate fecundity would be somewhat along a continuum between these aforementioned extremes. But, as pointed out by Wilbur, Tinkle, and Collins (1974), trophic level and environmental predictability should be considered in addition to fe-

cundity in viewing organisms in relation to the r and K continuum.

Only the most obvious examples of trophic level can be used here with any degree of certainty. Generally anurans are insectivorous and are opportunistic feeders on any available prey small enough to swallow. Most tadpoles are grazers or planktonic filter-feeders. But there are some notable exceptions. *Ceratophrys* and *Hemiphractus* generally prey on terrestrial vertebrates, and *Leptodactylus pentadactylus* takes some small frogs. The aquatic *Pipa* feeds on fish, and the tadpoles of *Ceratophrys* are carnivorous. With the exception of *Dendrobates* and *Phyllobates*, which, due to their skin toxins, are distasteful to potential predators, the smaller species of frogs and the young of the larger species are at a low trophic level in the community. Spiders, mammals, birds, and especially snakes feed heavily on frogs, and some species of snakes feed exclusively on frogs.

Environmental stability is difficult to measure, so again only obvious differences can be evaluated. Assuming that predictability is positively correlated with environmental stability, we can view the primary rainforest as the most stable terrestrial habitat at Santa Cecilia. Some species, such as *Bufo marinus*, *Hyla rubra*, *Leptodactylus mystaceus*, and *Eleutherodactylus variabilis* are colonizing species in non-primary forests. Another 16 species (11 *Hyla* plus one each of *Phrynohyas*, *Phyllomedusa*, *Leptodactylus*, *Physalaemus*, and *Rana*) are peripherally pioneering species. All of the others are generally restricted to primary forest. We can view the colonizing species as existing in the least predictable environments and the pioneering species as inhabitants of somewhat more predictable habitats. If we consider frogs having the generalized reproductive mode (Mode 1) to be characteristic of "r-strategists" and species with the more advanced reproductive modes characterized by lower fecundity and

TABLE 17.—Environmental Predictability and Reproductive Modes in Anurans. (Numbers are species.)

MODE	Colonizers	Pioneers	Climax
1	2	9	24
2	---	---	1
3	---	1	---
4	---	4	6
5	---	---	3
6	1	2	6
7	---	---	6
8	---	---	1
9	1	---	17
10	---	---	1
11	---	---	1

presumably higher survivorship to be "K-strategists," we find disproportionate numbers of "r-strategists" among the colonizing and pioneering species as compared with those primarily or exclusively inhabiting climax forest. (Table 17). This suggests that high fecundity is important to survivorship in unpredictable environments, whereas low fecundity with or without parental care is a strategy suitable to more predictable environments.

The extremes in reproductive strategies in this community seem to be *Bufo marinus* at the "r" end of the continuum and *Hemiphractus probosideus* at the "K" end. *Bufo marinus* lays clutches of more than 10,000 eggs, apparently breeds more than once a year in ephemeral ponds in non-primary forest habitats, and has a very large ovarian size factor (110.2). The small eggs and tadpoles have short periods of development, but many desiccate. Very young toads are a food source for a variety of predators; adults prey on a variety of arthropods. Contrarily, *Hemiphractus* apparently breeds only once each year, has clutches of less than 30 large eggs developing on the back of the female, and an ovarian size factor of 1.0. The adults prey on large orthopterans, frogs, and lizards.

Modifications of the generalized pond breeding reproductive mode all seem to be directed towards increased survivorship of the eggs and/or larvae.

This is accomplished by multiple small clutches, removal of eggs and/or tadpoles from water, and/or parental care. Increased reproductive specialization results in reduced fecundity but increased survivorship. Reproductive generalists with high fecundity are better adapted for unpredictable environments.

Lizards

Tinkle, Wilbur, and Tilley (1970) distinguished two major reproductive strategies in lizards: 1) species that mature early and have multiple broods annually, and 2) species that mature late and have single broods annually. Their definition of reproductive strategies was based on an analysis of 37 species of lizards in six families from diverse environments. In contrast to late-maturing lizards, they stated that in early-maturing lizards: 1) oviparity is nearly universal, 2) nearly all have multiple broods, 3) mean clutch size is significantly smaller, 4) most of the variance in clutch size between species is accounted for by consideration of size and age at first breeding, 5) they are smaller-bodied at maturity, and 6) they tend to be tropical and temperate in distribution, as opposed to primarily temperate for late-maturing single-brooded lizards. Tinkle, Wilbur, and Tilley (1970) suggested that clutch-size in the tropics is adjusted differently than in temperate species and that high intraspecific competition in the tropics results in selection for smaller clutches of large eggs with greater survivorship than larger clutches of smaller eggs. Andrews and Rand (1974) in their study of reproduction in *Anolis* disagreed with Tinkle, Wilbur, and Tilley (1970) and emphasized that there is no evidence for larger eggs in tropical lizards than in temperate species and that higher competition in tropical than in temperate lizards has not been demonstrated. Furthermore, Andrews and Rand (1974) suggested that clutch size is small in *Anolis* (and probably in many other tropical lizards) in correlation with

more frequent oviposition rather than large egg size.

In reviewing the reproductive strategies of the lizard comprising the community at Santa Cecilia, I am considering the following factors: 1) phylogenetic limitations, 2) structural habitat, and 3) escape mechanisms, all with respect to female body size, clutch size, and frequency of oviposition. A basic assumption is that gravid lizards are less agile; therefore survivorship is enhanced if females are not overburdened with eggs for lengthy periods of time.

Gekkonid lizards (*Gonatodes*, *Pseudogonatodes*, and *Thecadactylus* at Santa Cecilia) always have one or two mature ova; this is a reproductive characteristic inherent in the family and does not appear to be influenced by structural habitat, environmental factors, or escape mechanisms. Gekkonids as a group are early maturing, multiple-brooded lizards; the majority of the species occur in the tropics, but many, if not most, species inhabit arid or semi-arid regions. The only viviparous lizard at Santa Cecilia, *Mabuya mabouya*, belongs to a genus having both oviparous and viviparous species; generally *Mabuya mabouya* inhabits more seasonal environments than that characteristic of Santa Cecilia. Similarly, *Ameiva ameiva*, the only lizard in the community definitely known to have cyclic reproduction, primarily is an inhabitant of seasonal environments.

Small clutch size is the rule in microteiid lizards, all of which at Santa Cecilia are small fossorial or terrestrial species (maximum snout-vent length of 79 mm in females). In these small lizards, as in the gekkonids, clutches of one or two eggs apparently are well established evolutionary traits.

Andrews and Rand (1974) argued that the small clutch size in *Anolis* can be attributed to their arboreal habits; they reasoned that the specialized climbing adaptations of anoles (adhesive digital lamellae) limit the load-bearing capacity of the lizard. They noted that

orboreal gekkonids, which also have adhesive digital lamellae, have small clutches, whereas arboreal lizards, such as *Polychrus* and *Iguana*, which rely on strong claws for climbing, have larger clutches. If we examine the arboreal lizards at Santa Cecilia, we find that all of those having adhesive digital lamellae (2 gekkonids and 6 *Anolis*) have no more than two mature ova at once, whereas the arboreal species lacking adhesive lamellae but relying on strong claws (*Enyalioides laticeps*, *Plica umbra*, *Polychrus marmoratus*, and *Uracentron flaviceps* have larger clutches (2-11, $\bar{x}=5.9$).

Foraging activity and escape mechanisms also need to be considered with respect to egg-laden females. Vitt and Congdon (1975) demonstrated that among the deserticolous lizards they studied, those species that forage close to shelter had a greater caloric value of eggs than those that run longer distances from foraging sites to shelter. Anoles normally escape by scampering through bushes or up trees, frequently leaping from one branch to another; obviously, agility is required. Therefore few oviducal eggs are advantageous. The slow-moving *Polychrus marmoratus*, which depends upon protective coloration to escape predators, has large clutches (7-11, $\bar{x}=9.3$), as does *Enyalioides laticeps* (5-7, $\bar{x}=6.3$), which escapes by moving around and slightly up trunks of saplings. In contrast, the terrestrial *Enyalioides cofanorum* with a clutch of two eggs, runs to cavities for shelter. Likewise, *Plica umbra* (clutch size 2-4, $\bar{x}=2.5$) forages on the ground and runs to trees for shelter. *Ameiva ameiva* and *Kentropyx pelviceps* are agile, terrestrial lizards. *Ameiva* frequently forages far from shelter, and it is not uncommon to observe a lizard running 20 m or more to shelter. On the other hand, *Kentropyx* forages in small clearings in the forest or on the forest floor and seldom runs more than 5 m to shelter. *Ameiva* has 2-6 ($\bar{x}=3.7$) eggs, whereas *Ken-*

tropyx has 4-6 ($\bar{x}=5.0$) eggs. The viviparous *Mabuya mabouya*, gravid females of which are heavily burdened with 4-6 ($\bar{x}=5.2$) young, forage and sun on logs, in or beneath which they seek shelter.

Studies on reproduction in a variety of tropical lizards by Marshall and Hook (1960), Inger and Greenberg (1966), Sexton and Turner (1971), Sexton *et al.* (1971), León and Ruiz (1971), and Andrews and Rand (1974) demonstrate that in seasonal environments, oviposition occurs during the rainy season, whereas in continuously wet tropical environments, oviposition is continuous, or nearly so, throughout the year. As noted by Tinkle, Wilbur, and Tilley (1970), lizards inhabiting the wet tropics generally are early maturing with multiple broods annually. One strategy of the early maturing lizards is to place a large hatchling in the environment. The ratio of snout-vent length of hatchlings to that of gravid females in ten species of lizards at Santa Cecilia is 37.4-43.2 ($\bar{x}=39.9$) percent. The ratios vary only slightly in different adaptive groups: 40.9 in *Gonatotodes*, 38.9-43.2 ($\bar{x}=40.4$) in three anoles, 37.5 in *Enyalioides laticeps*, 37.4-42.9 ($\bar{x}=40.3$) in three microteiids, and 39.1-39.2 in two macroteiids. Thus, the number of eggs in a clutch shows no significant correlation with the relative size of the hatchling, although those species having larger clutches have proportionately smaller hatchlings than do some of the species having smaller clutches.

Seemingly, reproductive strategies have evolved in order to provide the most effective input of young into the population. The production of young must be viewed over the reproductive life span of the female. Here, the aspect of risk becomes important (Tinkle, 1969). Obviously, the burden of oviducal eggs is risky to the gravid female; a small hatchling runs a greater predation risk than a larger one, and a late-maturing lizard runs a greater risk of

death prior to reproduction than does an early-maturing species. All of the restrictions must be balanced against an effort towards high fecundity. A reduction in clutch size is offset by increasing the number of clutches. A reduction in clutch size theoretically also can be offset by producing larger hatchlings that reach sexual maturity in a shorter period of time.

The reproductive strategies exhibited by the species comprising the community at Santa Cecilia can be summarized, as follows:

1. Early-maturing with multiple clutches
 - A. Small clutches inherent phylogenetically (possibly also due to load-bearing of adhesive lamellae) – gekkonids.
 - B. Small clutches primarily due to load-bearing of adhesive lamellae and need for agility – anoles.
 - C. Small clutches due to necessity of rapid escape – *Enyalioides cofanorum*, *Plica umbra*.
 - D. Small clutches because of restriction of body size – microteiids.
 - E. Large clutches possibly because of large size and slow movements – *Enyalioides laticeps*, *Polychrus marmoratus*, and *Kentropyx pelviceps*.
2. Late-maturing with single clutches
 - A. Smaller clutches due to necessity of rapid movements – *Ameiva ameiva*.
 - B. Larger clutches, viviparous – *Mabuya mabouya*.
 - C. Presumably in this group – *Dracaena*, *Tupinambis*, and *Uracentron*.

Snakes

Within the serpents there is a basic dichotomy of reproductive modes – oviparity versus viviparity. Neill (1964)

and Fitch (1970) addressed the two modes. In contrast to oviparous species, viviparous snakes generally have smaller broods and reproduce less frequently. Advantages to viviparity are the lack of need to find a suitable nest site and protection of the embryos from predators and unfavorable environmental conditions. A definite disadvantage to viviparity is the length of time that the female must carry the young and her susceptibility to predation while gravid. Neill (1964) emphasized the protection afforded the developing young of venomous species, and Fitch (1970) further noted that viviparity was most prevalent in heavy-bodied, slow-moving or aquatic snakes.

At Santa Cecilia viviparity occurs in the five species of boids and three species of *Bothrops*, all relatively heavy-bodied, sluggish snakes. The more slender *Lachesis muta* is the only species of erotolid known to be oviparous. Apparently the water snakes of the genus *Heliopsis* are facultatively oviparous or viviparous (Rossman, 1973.) Viviparity in these aquatic snakes eliminates the necessity of their leaving the water to deposit eggs. All other snakes at Santa Cecilia are oviparous.

Clutches are larger in the viviparous species than in the oviparous ones; this apparent contradiction is obviously due to the fact that the largest species in the community are viviparous. Among the oviparous species the heavy-bodied terrestrial snakes have larger clutches than the slender-bodied arboreal species. The latter certainly would be hampered in their movements by the burden of a large ovarian complement. Some slender terrestrial snakes (*Chironius* and *Dendrophidion*) may be similarly restricted.

DISCUSSION

Certain aspects of reproduction in the fauna have not been covered in the foregoing sections, either because they were not pertinent or because they in-

volved arguments or concepts not relevant to any one of the organized categories.

Reproduction in Other Groups

In order to complete the presentation of the data on groups not covered in the preceding accounts, the information is summarized here.

Caecilians.—Presumably all of the caecilians at Santa Cecilia are viviparous or at least oviparous with terrestrial eggs and no aquatic larvae. No information is available on annual reproductive patterns or fecundity.

Salamanders.—The two species of *Bolitoglossa* presumably lay terrestrial eggs like other members of this widespread Neotropical genus. *Bolitoglossa peruviana* has 6-13 ova maturing at one time, and the seasonal incidence of gravid females and young suggests that reproduction is acyclic.

Turtles.—According to local residents, at least some of the aquatic pleurodire turtles (*Chelus*, *Mesoclemmys*, *Phrynops*, and *Platemys*) deposit eggs on sand banks at times of low water in the Río Aguarico — usually in December; presumably only one clutch is laid per year. *Geochelone* also probably deposits only one clutch annually, but *Kinosternon* may have multiple clutches.

Crocodilians.—As a group, the Neotropical crocodilians apparently have single large clutches of eggs each year.

Reproductive Potential

The data on, and discussion of, fecundity are based almost exclusively on ovarian complements. Although these data are basic to certain aspects of our knowledge of the reproductive biology of the species involved and of the community as a whole, they neither provide a comprehensive picture of fecundity nor of reproductive potential. Also, in order to have a true picture of reproductive potential, it is necessary to know the reproductive life span of the females.

Andrews and Rand (1974) reported

that *Anolis limifrons* in Panamá lays one egg every 8.1 days; females reach sexual maturity in four months. Thus, based on survival data, each female has the potential for depositing about 18 eggs during her life. At Santa Cecilia *Anolis fuscoauratus* (a close relative of *A. limifrons*) and *A. trachyderma* are like *A. limifrons* in size and habitat. I suspect that the reproductive potential of these species is comparable with that of *A. limifrons*.

Crump (1974) reported one female of *Hyla rhodopepla* from Santa Cecilia deposited clutches of 390 and 260 eggs 31 days apart. If a given female reproduced at this rate for an entire year, she would produce only about 3900 eggs. This is a relatively small number of eggs, for some species, such as *Bufo marinus* have clutches in excess of 10,000 eggs. Obviously survivorship is extremely low in most high fecund lizards and frogs. For example, if all the eggs of a given clutch deposited by two pairs of *Bufo marinus* matured to adults, the resulting toads would completely cover one square kilometer.

General Conclusions

In a final consideration of the reproductive modes and strategies operant in a herpetological community in an aseasonal tropical rainforest, it must be borne in mind that, with possibly few minor exceptions, the mode of reproduction and strategy utilized by any given species evolved in that species prior to its inclusion in the present community. Thus, it is not reasonable to infer that a species evolved a certain reproductive mode or strategy in response to the presence of other species in the community as we know it today. Instead, each reproductive strategy is the result of selection for an effective means of producing a succeeding generation. The selective forces include, but are not necessarily restricted to adaptations for survival of eggs and young (including larvae) in unpredictable (sporadically fluctuating)

environments and the survival of gravid females against predation. Although reproductive potential may be high in many species, survivorship, especially of eggs, larvae, and young, is low, whereas survivorship is higher in species with lower fecundity. Although there are some exceptions, lower fecundity and higher survivorship probably are characteristic of species at higher trophic levels, species inhabiting the more predictable environments, and those with parental care.

In the aseasonal climatic regime at Santa Cecilia, reproduction in most species apparently is continuous, or nearly so. There is a continuous infusion of young into the population and overlapping generations. Continuity of successful reproduction tends to decrease population fluctuation. Increase in population fluctuation increases the rate of extinction (MacArthur and Wilson, 1963). Thus, as suggested by Inger and Greenberg (1966), the continuous breeding of the species in the community may be one of the reasons for high species richness in humid tropical rainforests.

Seasonal Versus Aseasonal Environments

Subsequent to Dobzhanky's (1950) suggestion that natural selection in the tropics favors lower fecundity and slower development, as opposed to higher fecundity and faster development in the temperate regions, the literary frenzy of evolutionary biologists has resulted in a monumental pile of publications offering multitudinous theories and comparatively few data (for a realistic appraisal of the situation, see MacArthur, 1972:216). Because seasonality is characteristic of temperate and some tropical environments, I confine my comparisons between the aseasonal tropical rainforest and seasonal environments, both tropical and temperate. Although the climatic regimes of temperate regions and extremely seasonal tropical regions, such as those having a monsoon climate are dissimilar, the effect on the biota is much the same.

Periods of activity are restricted, either directly or indirectly, due to cold or drought, and adverse periods (with the exception of non-migratory endothermal vertebrates) necessitate inactivity through hibernation or aestivation of adults, larvae, pupae, or zygotes.

In the case of amphibians and reptiles, a single clutch of eggs is characteristic of species inhabiting extreme seasonal environments, although the same species may produce more clutches in more equable parts of its range. Furthermore, reproductive maturity may not be attained for two or more years. Timing of breeding is usually dependent upon the presence of available moisture – rainfall in dry areas and thawing as well as temperature in cold areas. The timing of the production of eggs or young is not only critical with respect to the availability of suitable oviposition sites, but also to the availability of food for the young as well as the adults. Also, it is necessary that the young have sufficient time to build up an adequate fat supply to carry them through the forthcoming period of inactivity. Amphibians and reptiles have evolved diverse adaptations for those adverse climatic regimes, including autumnal fertilization, overwintering of tadpoles and hatchlings, and viviparity in squamates in temperate climatic regimes, and rapid development of ova and larvae and cunning ways to conserve bodily fluids in monsoon tropical areas.

These kinds of environmental stresses are minimized or non-existent in equable humid tropical rainforests. Aperiodic fluctuations in rainfall may result in the desiccation of eggs or larvae, but aperiodic fluctuations are even more frequent in the other climatic regimes. Consequently, in populations where all sexually mature adults breed simultaneously, the elimination of one generation is not an uncommon phenomenon in extremely seasonal environments. By comparison, in the tropical rainforest where only a fraction of the adults are

breeding at any one time, the elimination of their offspring will not be nearly so catastrophic for the population.

The advent of aperiodic climatic fluctuations will have a more profound effect on population fluctuation in species in seasonal environments than in the aseasonal tropical rainforests. Population size is more uniform in the tropical rainforests than in the seasonal environments. The continuous activity of non-fluctuating populations lends greater stability to the biotic environment in an aseasonal tropical rainforest than is possible in areas with highly seasonal climatic regimes.

Because of greater varieties of structural habits and more equable environmental conditions, amphibians and reptiles in aseasonal tropical rainforests have exploited a wider array of reproductive strategies than they have in temperate and seasonal tropical areas. This is especially true among anurans, which at Santa Cecilia are represented by 11 modes of reproduction; only the primitive Mode 1 is found in frogs inhabiting extremes of seasonal environments. Salthe and Duellman (1973) noted the diversity of reproductive modes in tropical anurans and suggested that small frogs, into which general category most tropical frogs can be placed, are pre-adapted for evolutionary exploration of new reproductive modes.

Although clutch or brood size usually is larger in species in seasonal environments than in comparable species in aseasonal tropical environments, breeding is more frequent in the species in the aseasonal areas, or increased parental care in specialized reproductive modes in the tropics presumably results in greater survivorship. Thus, it is unlikely that any generalities about higher fecundity in the temperate regions have any validity. Likewise, developmental time in ectothermal tropical species is likely to be shorter in the warm tropical regime than in the cooler temperate environments. Of course, this comparison

must be made within a given reproductive mode.

In summary, amphibians and reptiles in aseasonal tropical rainforests employ a wider array of reproductive strategies, reproduce more frequently, mature earlier, and have more stable populations, but probably have lower survivorship and shorter life spans than do their coun-

terparts in seasonal environments. The apparently complete absence of pair bonds combine with frequent mating and reproduction results in a greater genetic mixing, which, in addition to the diversity of structural habitat and vast array of other available resources provides the potential for rapid differentiation and subsequent speciation.

COMMUNITY STRUCTURE

Although MacArthur (1971) defined a community as "any set of related organisms near each other and about which it is interesting to talk," in reality a community consists of all of the organisms that live together in a particular place. Usually only portions of communities are studied, and most frequently the division is taxonomic. Thus, the present analysis of the herpetological community is unusual only in the species richness of the community.

In order to study a community it is necessary to measure various parameters. A major weakness inherent in this approach is that we measure those features that we think are important, but our inability to view the environment from the eyes of the organism imparts a bias and certainly a gross incompleteness to resulting analyses. For example, the absence of temporal, spatial, and dietary differences in the available data on the three species of *Dipsas* at Santa Cecilia can only be interpreted reasonably as an absence of measurements of the ecological factors that are different in these snakes. The point here is that most analyses are not refined; certainly many more differences exist than are normally measured, and the differences generally can be interpreted as being greater than those indicated in the analyses.

Furthermore, unequal sampling in different habitats at different times results in biased data (see p. 13). Nonetheless, given these inadequacies of sampling and measurement, it is possible to provide a basic analysis of the herpe-

to faunal community. This analysis is more extensive than any heretofore attempted for a tropical rainforest herpeto-community.

Terms used herein are defined, and where appropriate, analytical techniques are discussed below.

Coefficient of Community.—This is Whittaker's (1970) mathematical measure of the relative similarity of samples from two communities:

$$CC = S_{ab} / (S_a + S_b - S_{ab}),$$

where S_{ab} is the number of species shared by samples A and B, S_a is the total number of species present in sample A, and S_b is the total number of species in sample B.

Ecological Allopatry.—Two or more species living in the same habitat but separated by differences in microhabitat or diel activity.

Ecological Sympatry.—Two or more species living in the same microhabitat and overlapping in their diel activity.

Habitat.—That major portion of the physical environment in which an organism carries out its life processes. As used here, habitats are major structural aspects of the area: forest, clearing, river, etc.

Habitat Generalists and Specialists.—These terms are used in the sense of Crump (1971). A habitat generalist is a species utilizing a broad spectrum of the environment; this can be determined from relative niche breadth scores. Habitat specialists are species living in a narrow range of the environmental spec-

trum; species that are not at the extremes of the continuum of habitat utilization are termed habitat intermediates.

Microhabitat.—This is a subdivision of the habitat. For example, within the primary forest habitat, the following microhabitats can be defined: fossorial, leaf litter, ground, bush, tree trunk, and canopy.

Niche.—This often maligned term is used in the sense of Hutchinson (1957) – an abstract concept of a multidimensional hypervolume. The dimensions are physical factors and biotic relationships necessary for the survival of the species.

Niche Breadth.—This term describes the spectrum of any given dimension of the niche hypervolume. The niche breadth of a species in a resource matrix can be measured by the methods suggested by Levins (1968) and modified by Colwell and Futuyma (1971) and Pianka (1972):

$$B_i = 1 / \sum_j p_{ij}^2,$$

where p_{ij} is the proportion of individuals of species i associated with resource j . Standardized niche breadth values (B_{ST}) can be obtained by dividing the niche breadth value (B) by the number or resource states.

Niche Overlap.—This is a measurement of the association of two or more species with respect to some dimension of the niche hypervolume. The niche overlap of two or more species in a resource matrix can be measured by the formula proposed by Colwell and Futuyma (1971):

$$C_{ih} = 1 - \frac{1}{2} \sum_j |p_{ij} - p_{hj}|,$$

where C is the amount of shared resource states between species i and h , p_{ij} is the proportion of individuals of species i associated with resource j , and h is the second species in the matrix. In this measure, C has a value of 0 when species i and h share no resource states and a maximum value of 1 when the proportional distributions of the two species

are the same. Combining overlap values from two or more independent analyses of different resources provides an overall niche overlap value. The overall values were obtained by multiplying for each pair of species the total of the individual niche overlap values times 100. This is the “product alpha” of Cody (1974).

Resource Partitioning.—The differential utilization of the physical and/or biotic environment by different species.

Species Diversity.—The concept of species diversity consists of two components – species richness and equitability. Species richness is solely the number of species, whereas equitability is a measurement of the evenness of distribution of individuals among species. Indices of species diversity were calculated by means of the information theory of Shannon (1948):

$$D = - \sum_i p_i \log_e p_i \approx$$

$$C/N \left(N \log_{10} N - \sum_i n_i \log_{10} n_i \right),$$

where p_i is the probability of encountering species i , C is the constant 3.321928 when using Base 2, N is the total number of individuals, and n_i is the number of individuals of species i . The formula describes an infinitely large population and results in the average diversity per species.

The ecological data recorded in the field, plus food and size recorded in the laboratory, were coded in the following categories.

A. Habitat:

1. Primary forest
2. Secondary forest
3. Forest-edge
4. Aquatic

B. Microhabitat:

1. Fossorial
2. Ground
3. Leaf-litter
4. Bush (<1.5 m)
5. Tree
6. Water

C. Activity Period:

1. Nocturnal
2. Nocturnal and Diurnal
3. Diurnal (shade)
4. Diurnal (sun)

D. Activity:

1. Sleeping
2. Resting
3. Moving
4. Feeding
5. Calling
6. Mating

E. Food:

1. Number of prey items in each taxonomic category
2. Size of largest prey item

F. Size:

1. Snout-vent length

For purposes of the computed similarity matrices and resulting distance phenograms, the modal code was used for each species, unless more than 25 percent of the individuals were found outside of the mode; in those cases combinatorial codes were used. Snout-vent lengths were coded by size classes: 1) ± 25 mm, 2) 26-50 mm, 3) 51-100 mm, etc. Prey items were coded by taxonomic category, except that arthropods were coded as "small" or "large"; ants and termites were coded separately in those species that feed exclusively on those items. For the anurans, five additional parameters were analyzed: 1) mode of reproduction (see Table 10); 2) calling site of males coded to modal site; and 3) three parameters of the mating call – note repetition rate, pulse rate, and dominant frequency. The phenograms were constructed from unweighted arithmetic means.

A general view of the community structure can be obtained by analyzing the three major taxonomic groups (anurans, snakes, lizards) independently (Figs. 172-174). Species of like size, habitat, diel activity, and food are grouped in these phenograms. Thus, amongst the lizards (Fig. 172), the small

forest-floor inhabitants are grouped at the top of the phenogram; arboreal species are in the middle, and larger terrestrial species are at the bottom. In the analysis of the snakes (Fig. 173), we find that most of those species in the upper half of the phenogram are diurnal terrestrial species, those just below the middle are primarily nocturnal arboreal species, and those at the bottom are aquatic. The introduction of reproductive parameters into the anuran analysis provides additional refinement (Fig. 174), so that most taxonomic groups fall out together in the phenogram – thus, all of the microhylids, dendrobatids, and centrolenids are grouped with other members of their families. On the other hand, larger and more diverse families have representatives in different parts of the phenogram. For example, large hyliids are separated from the small pond-breeding species, which are adjacent to the phyllomedusines, and all are widely separated from the carnivorous *Hemiphractus*. Likewise, among the leptodactylids, the groups that have aquatic larvae are separate from the small bush-dwelling *Eleutherodactylus*, which are disjunct from the larger terrestrial species.

These phenograms show the ecological relationships of any given species with other members of the same taxonomic category, but their information content is limited in that similarities are exaggerated. If similar data from Africa or Papua were interjected into the anuran phenogram, individual clusters would contain species from widely disparate regions, so that we would be analyzing the ecological similarities of allopatric species. To a lesser extent, the same thing is true of the analysis of the fauna at Santa Cecilia. Due to differences in habitat use there is ecological allopatry among the species in the community. Thus, it is necessary to examine the differences among ecologically sympatric species.

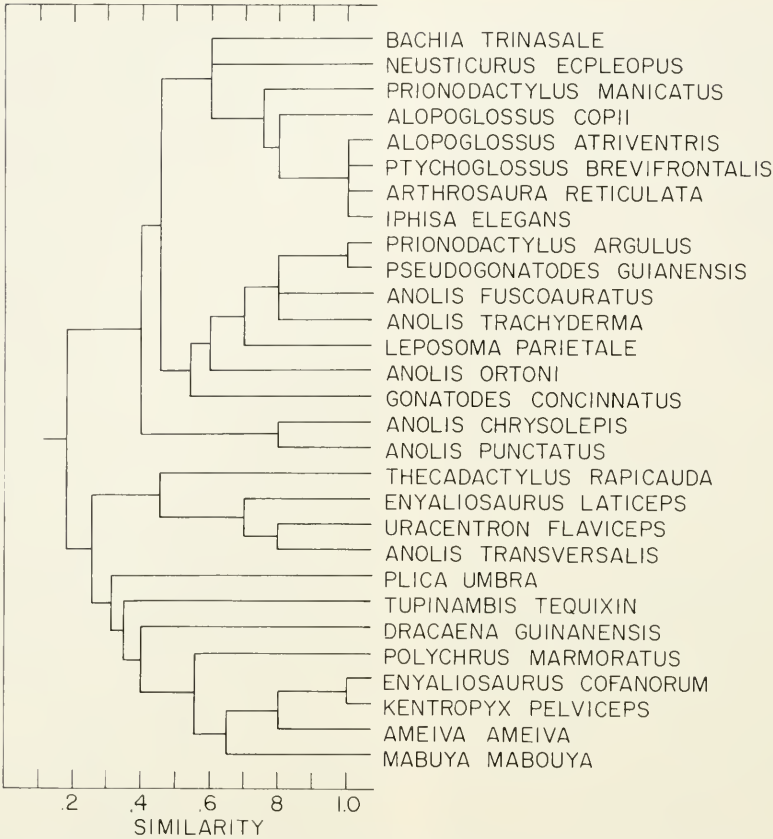


FIG. 172.—Modal resource utilization by lizards based on five parameters: habitat, vertical distribution, diel activity, food and size.

HABITAT ANALYSIS

Five major habitats can be discerned at Santa Cecilia – primary forest, secondary forest, forest edge, clearings, and aquatic sites. The latter includes all types of permanent and temporary ponds, streams, lakes, and rivers, all of which are interspersed within and between the terrestrial habitats and, thus, are not comparable with the terrestrial habitats. Only exclusively aquatic species are considered to be aquatic inhabitants; these include one amphibian and 11 reptiles: one anuran (*Pipa pipa*), four snakes (*Eunectes murinus*, *Helicops angulatus*, *H. petersi*, and *Micrurus surinamensis*), the two crocodilians, and five turtles (all except *Geochelone*).

Among the terrestrial habitats we find the greatest number of species in the

primary forest. Thirty-one species apparently are restricted to that habitat, whereas 12 are restricted to secondary forests, four to forest edges, and 13 to clearings. Comparisons of the inhabitants of the four terrestrial habitats were made by using Whittaker's (1970) measure of the coefficient of community (Table 18).

As would be expected, the greatest similarity exists between primary and secondary forests ($CC=0.680$). Generally, the secondary forest contains a slightly depauperate primary forest fauna. The apparent presence of certain species only in secondary forest may be an artifact of sampling; some of these species are not well represented in the collection. Others, such as *Eleutherodactylus variabilis*, *Hyla brevifrons*,

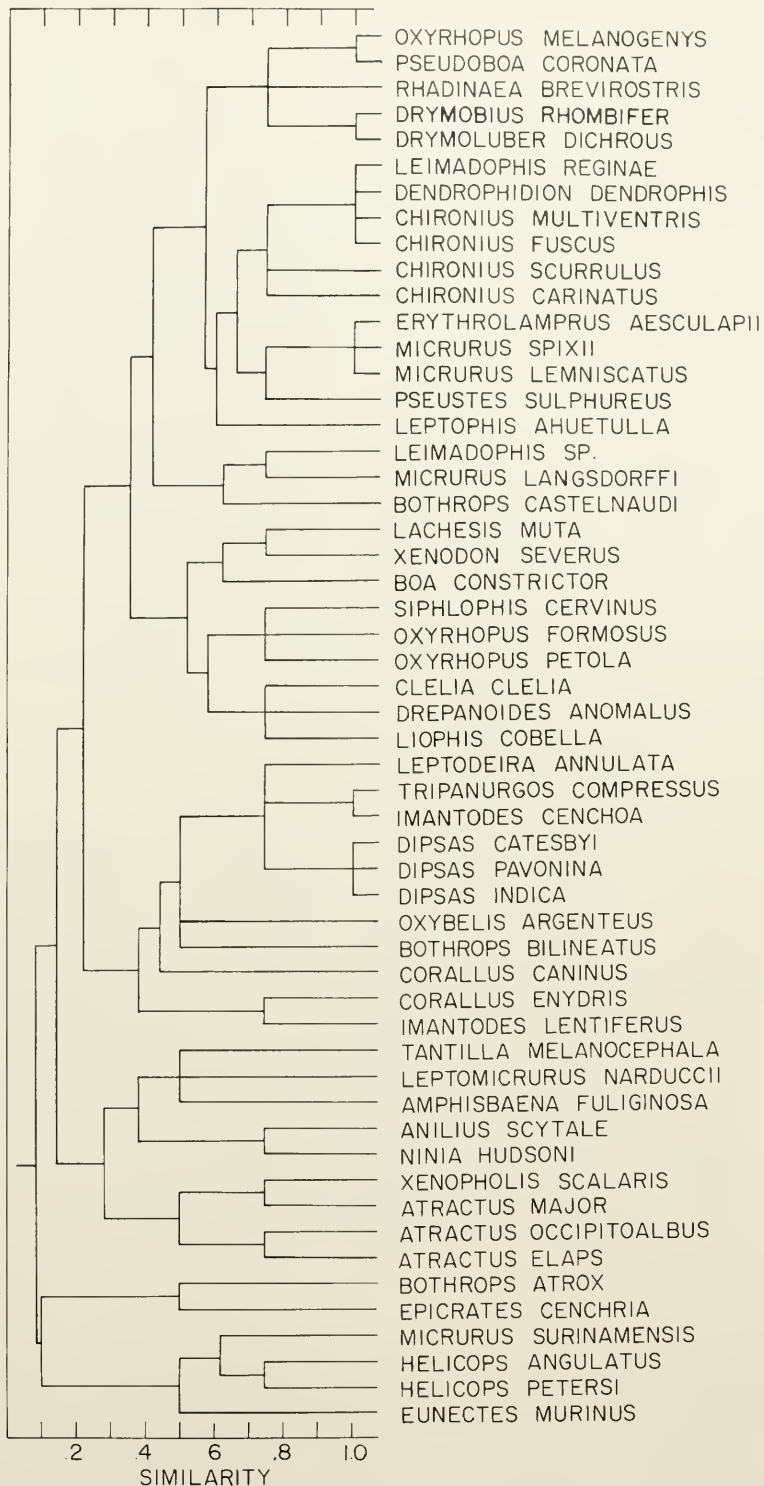


FIG. 173.—Modal resource utilization by snakes and amphisbaenians, based on four parameters: habitat, vertical distribution, diel activity, and food.

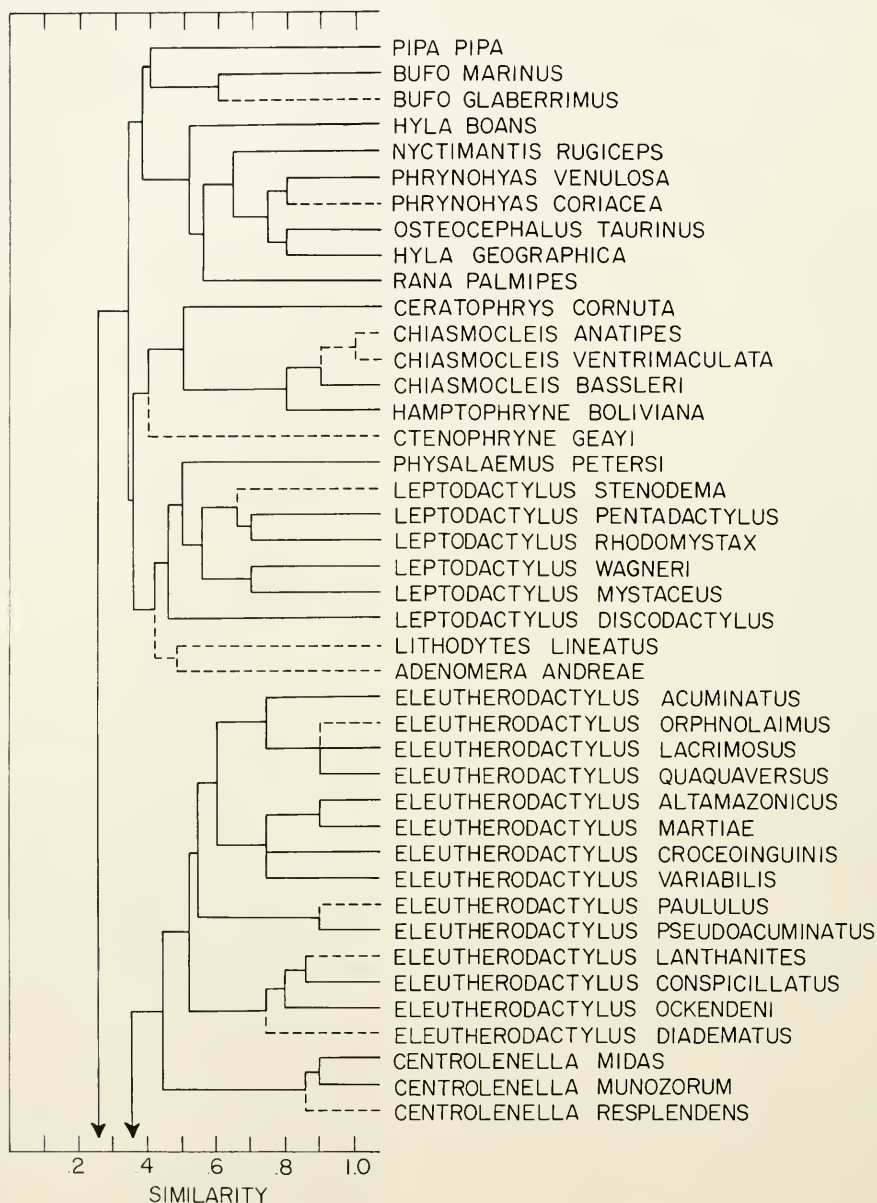


FIG. 174.—Modal resource utilization by anurans, based on five parameters: habitat, vertical distribution, diel activity, food and size (taxa indicated by dashed lines). Those taxa indicated by solid lines are arranged on ten parameters, in addition to the five above: mode of reproduction, calling site, note repetition rate, pulse rate, and dominant frequency of mating call.

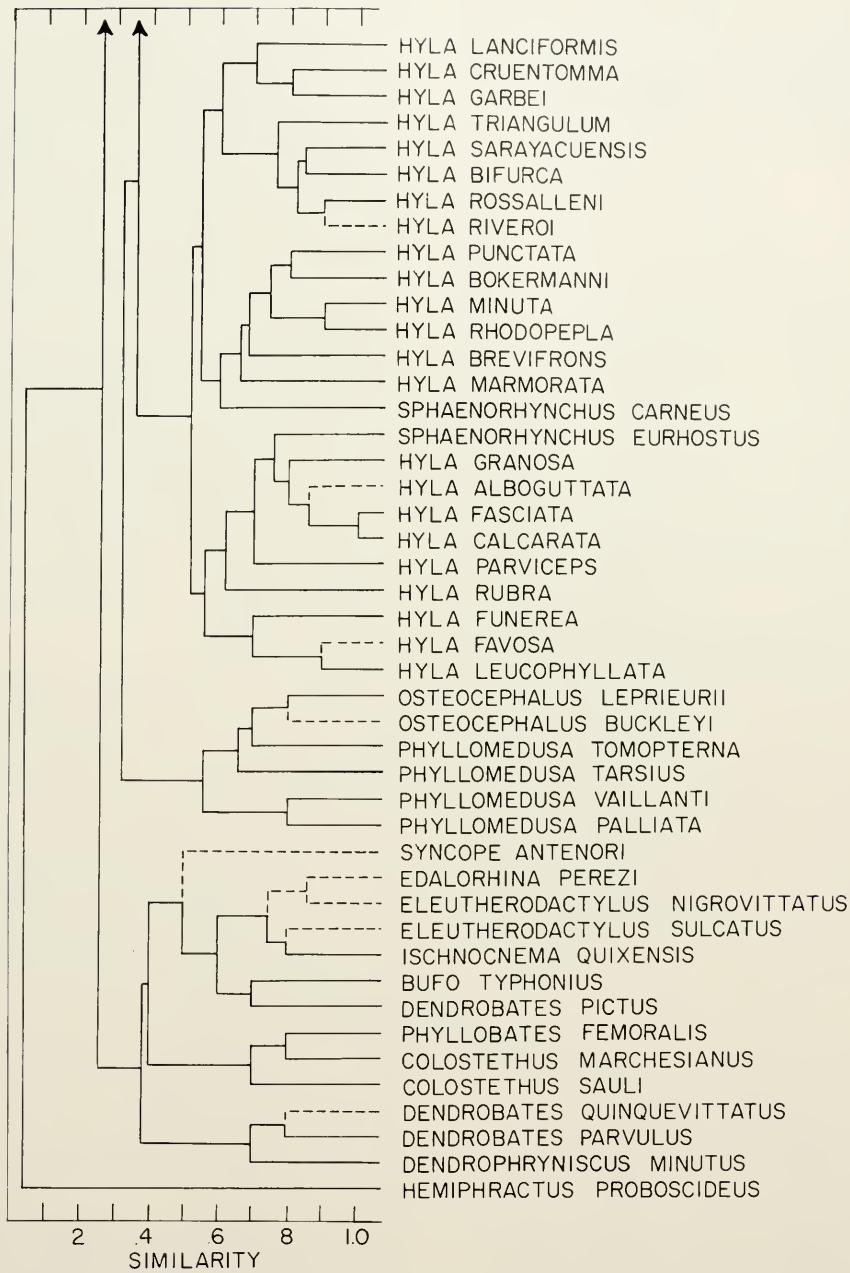


TABLE 18.—Comparison of the Herpetofauna in the Four Terrestrial Habitats at Santa Cecilia.

(Boldface numbers are the numbers of species occurring in a given habitat; Roman numbers are the numbers of species shared between two habitats, and italicized numbers are the community coefficients. See text for explanation.)

	Primary Forest	Secondary Forest	Forest Edge	Clearings
Primary Forest	134	102	8	8
Secondary Forest ..	.680	118	8	11
Forest Edge	.058	.065	12	8
Clearings	.053	.083	.285	24

Hyla cruentomma, *Hyla rhodopepla*, and *Imantodes lentiferus* are well represented in samples from secondary forest and absent in samples from primary forest and clearings.

Eight species have been found in primary and secondary forests and in clearings; these include five frogs (*Leptodactylus mystaceus*, *L. wagneri*, *Hyla bifurca*, *H. garbei*, *H. lanciformis*) and three snakes (*Chironius scurrulus*, *Oxyrhopus petola*, *Rhadinaea brevirostris*). One lizard (*Tupinambis tequixin*) and two snakes (*Boa constrictor*, *Bothrops atrox*) occur in secondary forest and clearings. These eleven species are the habitat generalists in the community.

Primary Forest

The primary forest is the most stable habitat at Santa Cecilia, and it can be viewed as the climax vegetation type in the area. Even so, it is a patchy environment in that differences exist in the amount of moisture and in the amount of shade. Slight variations in topography result in higher, better drained terrain with interspersed depressions that may contain water after heavy rains. Furthermore, the forest floor is dissected by numerous small permanent or intermittent streams. Tree falls create temporary areas receiving full solar radiation.

As noted previously, the primary forest is the richest habitat in numbers of species of amphibians and reptiles. The large fauna of 134 species can be divided conveniently into two assemblages – species that are terrestrial and those that are arboreal. Each of these assemblages can be subdivided into nocturnal and diurnal species. The following analysis excludes the fossorial caecilians and the aquatic turtles and crocodilians. Only one terrestrial turtle (*Geochelone denticulata*) occurs in the primary forest; it is diurnal and herbivorous. Each species is categorized by place and time of activity. Some species that occur on the ground and on bushes are included in two analyses; likewise, species that are active by day and night are included as members of both diurnal and nocturnal assemblages. On the other hand, species that are active on the ground but sleep in bushes and trees are treated in the terrestrial category.

Looking first at the terrestrial subcommunity in the primary forest, we find 43 diurnal and 18 nocturnal species (Figs. 175-176). The principal groups comprising the diurnal assemblage are microteiid lizards (9 species), dendrobatid frogs (5 species), leptodactylid frogs (6 species), racer-like snakes (8 species), and litter-dwelling snakes (8 species). Although the phenogram (Fig. 175) presents a general picture of the ecological relationships of the diurnal, terrestrial subcommunity in the primary forest, it is instructive to examine more closely the relationships of some groups within the subcommunity.

All of the microteiid lizards at Santa Cecilia are diurnal and inhabit primary forest. One species is fossorial (*Bachia trinasale*); the others are active on the forest floor (Fig. 177). Although these nine species are all similar in size and general habitat, they do exhibit differences in microhabitats and in food. *Neusticurus* occurs only along the margins of streams, and *Alopoglossus copii* prefers depressions that are more moist than the

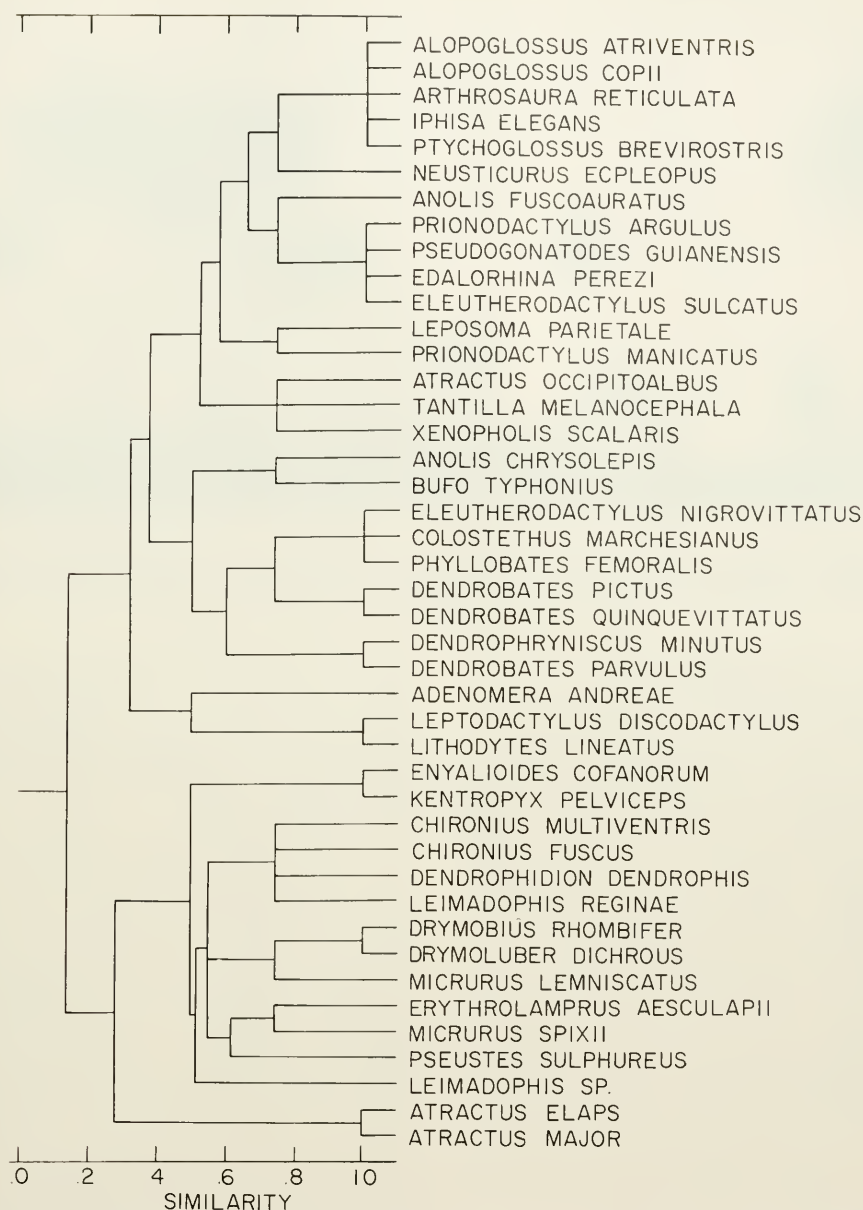


FIG. 175.—Modal resource utilization by diurnal terrestrial species in primary forest, based on substrate, shade versus sun, size, and food.

higher areas characteristically inhabited by the other microteiids. Among the latter, *Leposoma parietale* and *Prionodactylus maniculatus* are heliophiles, whereas the other five species usually are active only in deep shade. There are some obvious differences in the prey eaten by the microteiids (Table 19).

Taking into account various physical environmental parameters, plus food, niche overlap values were calculated by means of the formula proposed by Colwell and Futuyma (Table 20).

In the microteiid lizards the extreme mean overlap values of 35.69 (*Alopo-*
glossus atriventris) and 0.03 (*Ptycho-*

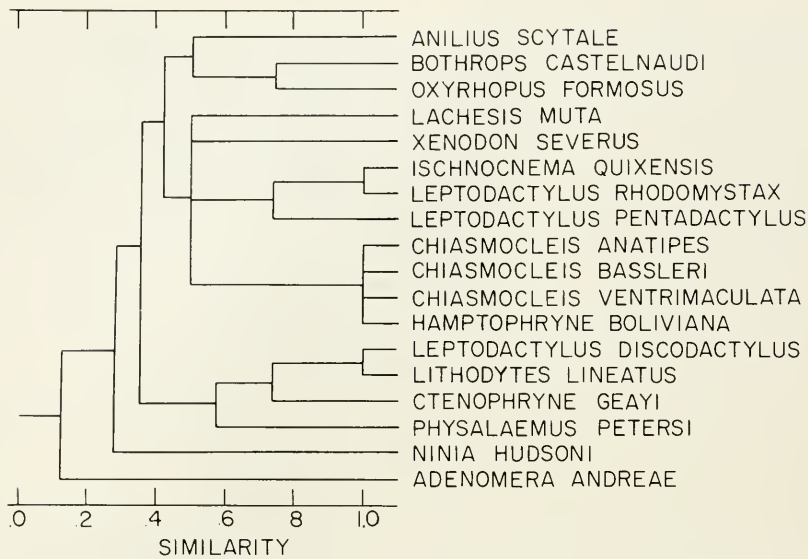


FIG. 176.—Modal resource utilization by nocturnal terrestrial species in primary forest, based on substrate, size, and food.

glossus brevifrontalis) are of limited meaning due to the absence of data on food. Among the other species, the fossorial *Bachia trinasale* has the lowest overlap value; with the other species, all of which are terrestrial. The other three terrestrial species active in deep shade have overlap values of 8.96-19.74 ($\bar{x}$ =12.69), and the two heliophilous species have an overlap value of 17.73. Excluding from consideration the two species with incomplete data we find that all pair-wise comparisons have values of less than 20. Thus, there is less than 20 percent overlap in total resource utilization by any pair of species of

microteiid lizards. Mean overlap values for other terrestrial forest lizards with the microteiiids are: *Pseudogonatodes guianensis* 8.32, *Anolis chrysolepis* 2.23, *Enyaliodes cofanorum* 6.69, and *Kentropyx pelviceps* 2.09. Thirteen species of frogs are active on the forest floor by day. These include five dendrobatids ranging in snout-vent length from 14.0 to 24.5 mm (mean lengths of males), six leptodactylids having snout-vent lengths of 18.5-39.3 mm, and two bufonids - *Dendrophryniscus minutus* (15.1 mm) and *Bufo typhonius* (58.7 mm). All of these are found most frequently amidst leaf litter; *Leptodac-*

TABLE 19.—Comparative Major Dietary Items (by volume) in Microteiid Lizards.

SPECIES	N	FOOD	
		Primary	Secondary
<i>Alopoglossus atriventris</i>	0	-----	-----
<i>Alopoglossus copii</i>	10	Arachnida (47%)	Orthoptera (30%)
<i>Arthrosaura reticulata</i>	6	Orthoptera (48%)	Isopoda (33%)
<i>Bachia trinasale</i>	6	Coleoptera (55%)	Oligochaeta (36%)
<i>Iplisa elegans</i>	1	Orthoptera (100%)	-----
<i>Leposoma parietale</i>	38	Formicidae (21%)	Hemiptera (21%)
<i>Neusticurus ecleopus</i>	25	Orthoptera (31%)	Arachnida (20%)
<i>Prionodactylus argulus</i>	20	Arachnida (46%)	Orthoptera (27%)
<i>Prionodactylus manicatus</i>	11	Arachnida (60%)	Orthoptera (22%)
<i>Ptychoglossus brevifrontalis</i>	0	-----	-----

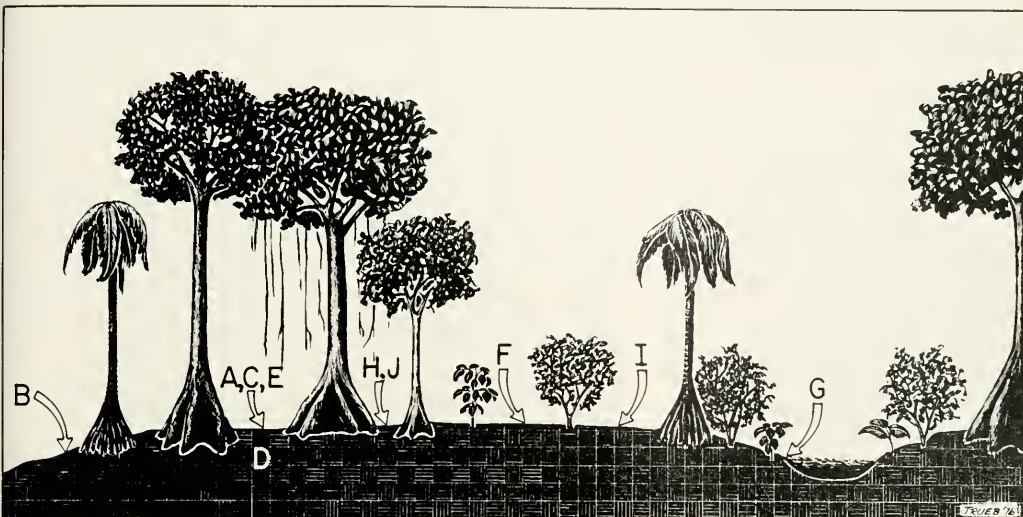


FIG. 177.—Microhabitats of ten species of microteïds at Santa Cecilia. A. *Alopoglossus atriventris*, B. *Alopoglossus copii*, C. *Arthrosaura reticulata*, D. *Bachia trinasale*, E. *Iphisa elegans*, F. *Leposoma parietale*, G. *Neusticurus ecleopus*, H. *Prionodactylus argulus*, I. *Prionodactylus manicatus*, J. *Ptychoglossus brevifrontalis*.

TABLE 20.—Niche Overlap Values for Microteïd Lizards.
(Product values $\times 100$ of four overlap values—habitat, substrate, vertical distribution, food; see text for explanation.)

	<i>Alopoglossus atriventris</i>	<i>Alopoglossus copii</i>	<i>Arthrosaura reticulata</i>	<i>Bachia trinasale</i>	<i>Iphisa elegans</i>	<i>Leposoma parietale</i>	<i>Neusticurus ecleopus</i>	<i>Prionodactylus argulus</i>	<i>Prionodactylus manicatus</i>	<i>Ptychoglossus brevifrontalis</i>
<i>Alopoglossus atriventris</i> ^a										
<i>Alopoglossus copii</i>	9.86									
<i>Arthrosaura reticulata</i>	100.00	2.66								
<i>Bachia trinasale</i>	10.98	0.00	0.00							
<i>Iphisa elegans</i>	64.00	3.84	8.96	0.00						
<i>Leposoma parietale</i>	42.53	8.36	11.90	0.74	3.05					
<i>Neusticurus ecleopus</i>	4.97	4.30	1.09	0.21	1.69	4.15				
<i>Prionodactylus argulus</i>	44.82	19.74	15.05	0.51	9.38	31.62	5.74			
<i>Prionodactylus manicatus</i>	45.06	14.00	11.72	0.07	6.11	17.73	2.20	43.02		
<i>Ptychoglossus</i>										
<i>brevifrontalis</i> ^a	0.00	0.00	0.00	0.02	0.00	0.13	0.00	0.09	0.00	
MEAN OVERLAP	35.69	6.97	16.82	1.39	10.78	13.28	2.71	18.89	15.55	0.03

^a Exclusive of food.

TABLE 21.—Comparative Major Dietary Items in Diurnal Terrestrial Frogs in Primary Forest.

SPECIES	N	Size Ratio	FOOD	
			Primary	Secondary
<i>Bufo typhonius</i>	25		Formicidae (88%)	Coleoptera (10%)
<i>Lithodytes lineatus</i>	9	1.49	Formicidae (42%)	Hemiptera (12%)
<i>Eleutherodactylus sulcatus</i>	15	1.16	Orthoptera (48%)	Chilopoda (20%)
<i>Edalorhina perezi</i>	4	1.00	Diptera (50%)	Orthoptera (25%)
<i>Leptodactylus discodactylus</i>	8	1.30	Coleoptera (41%)	Orthoptera (12%)
<i>Adenomera andreae</i>	11	1.04	Formicidae (35%)	Orthoptera (19%)
<i>Phyllobates femoralis</i>	21	1.02	Arachnida (15%)	Coleoptera (14%)
<i>Dendrobates pictus</i>	26	1.21	Formicidae (70%)	Coleoptera (10%)
<i>Dendrobates parvulus</i>	23	1.04	Formicidae (62%)	Coleoptera (18%)
<i>Eleutherodactylus nigrovittatus</i>	4	1.05	Coleoptera (39%)	Formicidae (22%)
<i>Colostethus marchesianus</i>	25	1.07	Formicidae (33%)	Coleoptera (28%)
<i>Dendrophryniscus minutus</i>	25	1.15	Formicidae (87%)	Coleoptera (3%)
<i>Dendrobates quinquevittatus</i> ..	1	1.08	Formicidae (100%)	

tylus discodactylus inhabits swampy areas, but the other species characteristically occur on higher ground. Although ants are the most common item in the diets of these 13 species, comprising 41 percent of the volume of food (Table 21), niche overlap values for prey items in the 13 species vary from 0.050 to 0.875 ($\bar{x}$ =0.482) (Table 22). Analysis of only the five species of dendrobatids provides mean niche overlap values of 0.438 to 0.650; these values are exceeded by the overlap of *Dendrophryniscus minutus* with the five dendrobatids – 0.535-0.825 ($\bar{x}$ =0.661).

Food data are available for 11 of the 16 species of snakes, each of which is narrow in its dietary preferences: insects 1, earthworms 3, frogs 3, lizards 2, snakes 1, mammals 1.

The nocturnal terrestrial assemblage in the primary forest consists of 12 frogs and six snakes (Fig. 176). The frogs comprise four groups: 1) the large beetle-eating microhylid *Ctenophryne geayi*, 2) the four small primarily ant-eating microhylids, 3) the small termite-eating leptodactylid *Physalaemus petersi*, and 4) the six larger leptodactylids that eat a wide range of arthropods. The four small microhylids primarily eat ants, but they also ingest some Coleoptera, Dermaptera, and Isoptera. Niche overlap values for food in these four species are 0.450-1.000 ($\bar{x}$ =0.699). *Hampto-*

phryne and the three species of *Chiasmocleis* have been found in the same small area ($\pm$ 1 hectare) on the same night. The six species of leptodactylids range from the small *Adenomera andreae* (average snout-vent length, δ δ =25.1 mm) to *Leptodactylus pentadactylus* ($\bar{x}$ =154.5). Niche overlap values for food in these six species are 0.125-0.720 ($\bar{x}$ =0.393).

Of the nocturnal terrestrial snakes, one feeds on mammals, one on lizards, one on caecilians, and two on frogs.

The analysis of the large arboreal herpetofauna in the primary forest is most readily accomplished by distinguishing "bush" inhabitants from "tree" inhabitants and each category separated into diurnal and nocturnal groups. Bush inhabitants are those species that characteristically are active in the lower strata of woody and herbaceous vegetation within 1.5 m of the ground. Tree inhabitants are those that occupy the higher woody vegetation and tree trunks. Some species occur on trees and bushes and are included in both analyses. The higher strata in the primary forest is extremely difficult to sample; the data on the amphibians and reptiles from there probably are incomplete.

Diurnal bush inhabitants include five lizards and three snakes (Fig. 178). Three of the lizards (*Anolis fuscoauratus*, *A. trachyderma*, and *Plica umbra*)

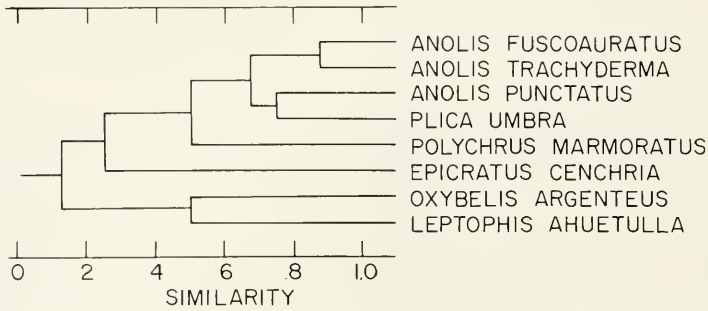


FIG. 178.—Modal resource utilization by diurnal bush inhabitants in primary forest, based on substrate, shade versus sun, size, and food.

also forage on the ground, and one snake (*Epicrates cenchria*) probably forages more on the ground than in bushes. Utilizing mean snout-vent lengths of males, we find two small lizards (*Anolis fuscoauratus*, 43.4 mm; *A. trachyderma*, 48.9 mm), two medium lizards (*Anolis punctatus*, 79.0 mm; *Plica umbra*, 83.1 mm), and one large lizard (*Polychrus marmoratus*, 115.0 mm). The two small *Anolis* feed on a variety of small arthropods and have a niche overlap value of 0.65 for food resources. *Anolis punctatus* also preys on a variety of arthropods, usually larger insects, and has niche overlap values for food resources of 0.54 and 0.28 with *A. fuscoauratus* and *A. trachyderma*, respectively. Although all three species are preying on similar kinds of food, their actual overlap is probably much less than that indicated by the foregoing values, due to terrestrial foraging activity of the two smaller species. *Plica umbra* feeds exclusively on ants and has niche overlap values for food resources of 0.00-0.28 (highest with *A. punctatus*) with the other bush-inhabiting lizards. *Polychrus marmoratus* primarily feeds on large orthopterans and has niche overlap values for food resources of 0.00-0.43 (highest with *A. punctatus*) with the other lizards. The *Anolis* utilize small perches, whereas *Plica* and *Polychrus* usually are on branches. *Epicrates cenchria* differs from the other snakes by eating mammals; this species is also active at night,

when it probably is feeding. *Oxybelis argenteus* feeds on lizards and frogs, and *Leptophis ahuetulla* apparently eats only frogs. The presence of these diurnal snakes suggests that the snakes are capable of finding frogs in their diurnal retreats, or perhaps they are crepuscular in their feeding schedules.

In the diurnal tree-inhabiting category, *Oxybelis* and *Leptophis* are the only snakes (Fig. 179). The small species of *Anolis* from the bush-inhabiting group are absent, but two larger lizards are present. *Anolis transversalis* (71.5 mm) feeding exclusively on orthopterans, and *Uracentron flaviceps* (123.0 mm) feeding only on coleopterans, occur in the canopy. The other tree-inhabiting lizards are restricted to trunks – saplings for *Enyalioides laticeps* and bases of large trees for *Gonatodes coninnatus* and *Anolis ortonii*.

The mean product values of niche overlaps of four parameters for the arboreal lizards are small (Table 23). The only values exceeding 6.0 are for the overlap of the three small *Anolis*. Thus, with the possible exception of these three species, the diurnal arboreal lizards are well segregated from one another ecologically.

By comparison with the diurnal arboreal assemblage, the nocturnal arboreal one is much larger and consists principally of anurans rather than lizards (Fig. 180-181). Many of the anurans

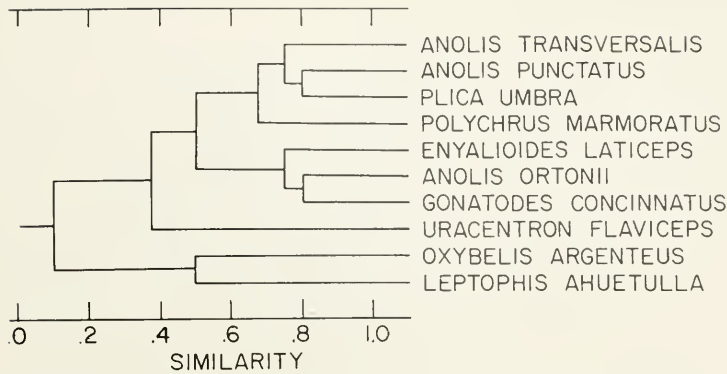


FIG. 179.—Modal resource utilization by diurnal tree inhabitants in primary forest, based on substrate, size, and food.

found on bushes at night retreat to cover in the trees by day; this is especially true for the hylids, most of which move from trees to low vegetation around ponds after rains.

Frogs of the genus *Eleutherodactylus* probably more accurately reflect the utilization of the bush habitat at night. Some of these species seek diurnal shelter amidst leaf litter on the ground, and others have diurnal retreats in the trees. However, they do not congregate at ponds for breeding; instead they remain in rather circumscribed areas. Most in-

dividuals of the 12 species of *Eleutherodactylus* perch on leaves 0.5-1.5 m above the ground. The mean snout-vent lengths of adult males is 15.0-30.4 mm and for adult females, 18.5-44.6 mm. The size ratios fall below the scale of 1.2-1.5 proposed by Hutchinson (1958) and Schoener (1970) (Fig. 182). All of the *Eleutherodactylus* feed on small arthropods, and with few exceptions they are catholic in their diets, resulting in high niche overlap values for food resources (Table 24). *Eleutherodactylus acuminatus* is the most distinctive in diet; 90

TABLE 23.—Niche Overlap Values for Arboreal Lizards.
(Product values $\times$ 100 of four overlap values—habitat, substrate, vertical distribution, food; see text for explanation.)

	<i>Gonatodes concinnatus</i>	<i>Anolis fuscoauratus</i>	<i>Anolis ortonii</i>	<i>Anolis punctatus</i>	<i>Anolis trachyderma</i>	<i>Anolis transversalis</i>	<i>Enyalioides laticeps</i>	<i>Plica umbra</i>	<i>Uracentron flaviceps</i>
<i>Gonatodes concinnatus</i>									
<i>Anolis fuscoauratus</i>	5.67								
<i>Anolis ortonii</i>	1.64	21.51							
<i>Anolis punctatus</i>	0.00	0.27	0.00						
<i>Anolis trachyderma</i>	5.65	37.33	13.09	0.00					
<i>Anolis transversalis</i>	2.27	0.09	0.00	0.00	0.00				
<i>Enyalioides laticeps</i>	3.85	1.33	0.85	0.00	2.42	0.50			
<i>Plica umbra</i>	0.04	0.00	0.68	0.00	0.00	0.00	0.00		
<i>Uracentron flaviceps</i>	0.00	0.00	0.00	0.00	0.00	0.00	3.95	0.00	
MEAN OVERLAP	2.39	7.04	4.72	0.03	7.31	0.36	1.61	0.09	0.49

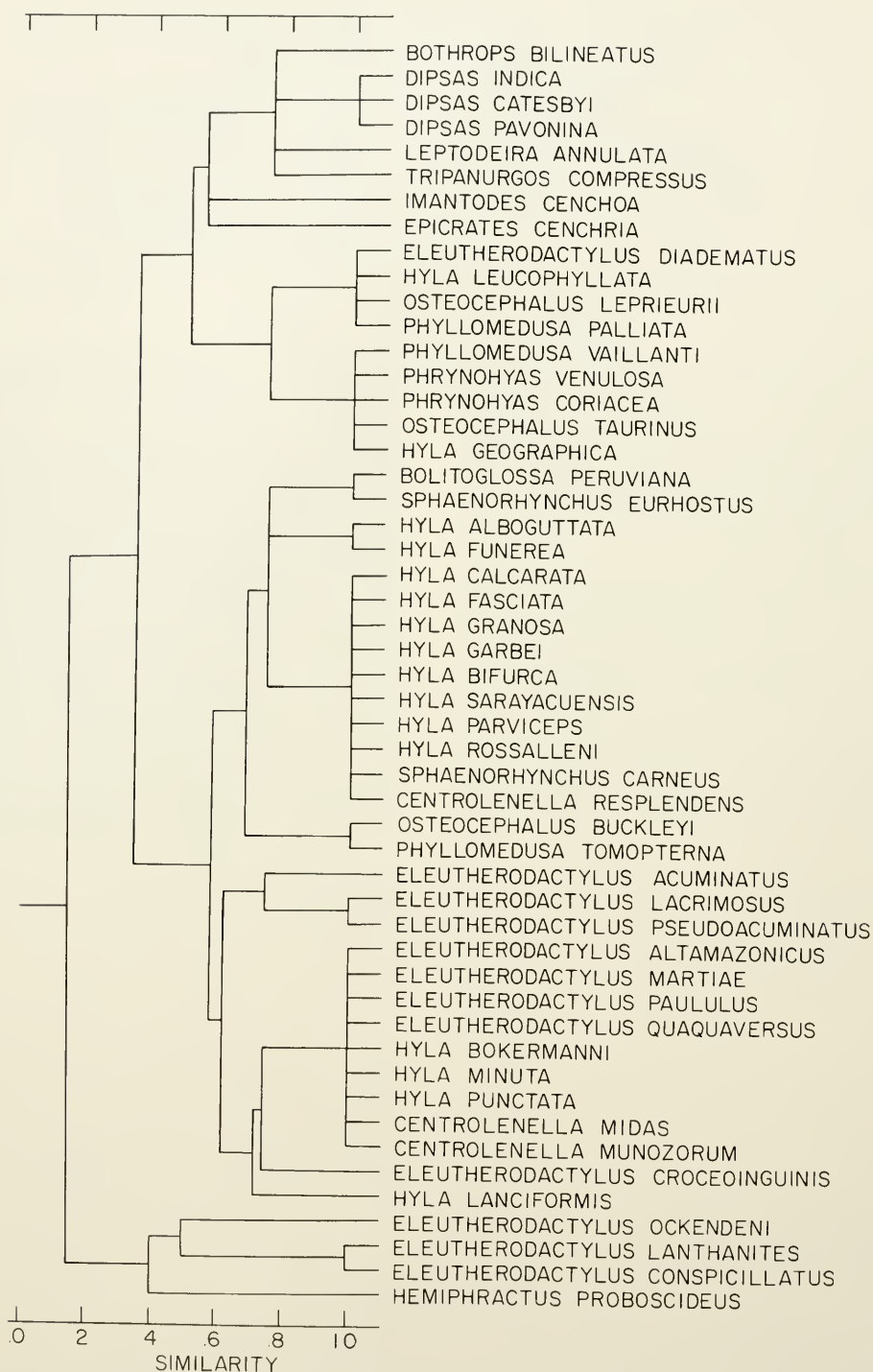


FIG. 180.—Modal resource utilization by nocturnal bush inhabitants in primary forest, based on substrate, size, and food.

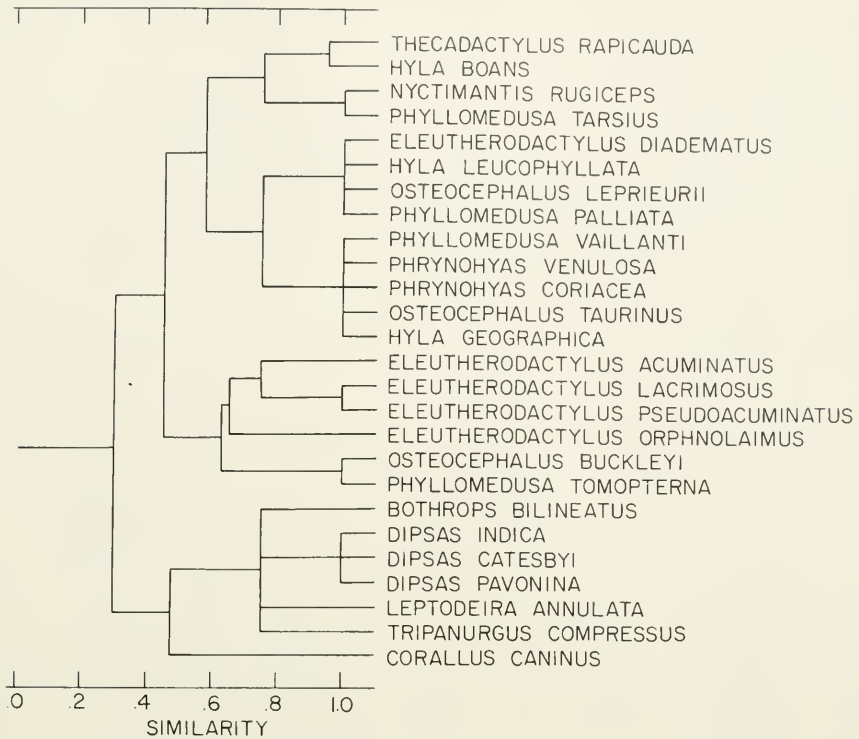


FIG. 181.—Modal resource utilization by nocturnal tree inhabitants in primary forest, based on substrate, size, and food.

percent of its prey is ants. The diet of *E. paululus* consists of 60 percent dipterans, and that of *E. lathanites* is 50 percent orthopterans. No one prey item makes up more than 30 percent of the diet of the other nine species.

Three of the remaining anurans are centrolenids and usually are on vegetation overhanging streams. The other 34 species are hylids, all but four of which prey on a variety of arthropods, principally orthopterans. In six species of hylids, orthopterans comprise more than 75 percent of the prey consumed, and in all hylids they make up 0.0-100.0 ($\bar{x}$ = 38.4) percent of the diets. The two species of *Sphaenorhynchus* prey exclusively on ants; *Hyla minuta* feeds primarily on lepidopteran larvae, and *Hyla riveroi* eats dipterans. Although *Hemiphractus proboscideus* eats some large orthopterans, it preys primarily on frogs.

The small salamander, *Bolitoglossa*

peruviana, apparently takes refuge in the leaf litter by day and ascends low herbaceous vegetation at night; the diet consists almost entirely of small ants.

Of the eight species of snakes, the three species of *Dipsas* are highly specialized snail-eaters; *Leptodeira annulata* is a voracious frog-eater and even consumes the arboreal eggs of *Phyllomedusa*. *Imantodes cenchoa* and *Tripanurgus compressus* feed on diurnal lizards, which presumably are found while they are sleeping; *Bothrops bilineatus* eats frogs, and *Epicerates cenchria* preys on small mammals.

The nocturnal, tree-inhabiting group essentially is a small version of the bush subcommunity; many of the small species of *Hyla* and *Eleutherodactylus* are absent as are *Centrolenella*, *Sphaenorhynchus*, and *Bolitoglossa*. As noted previously, the apparent absence of some species may be due to inadequate sam-

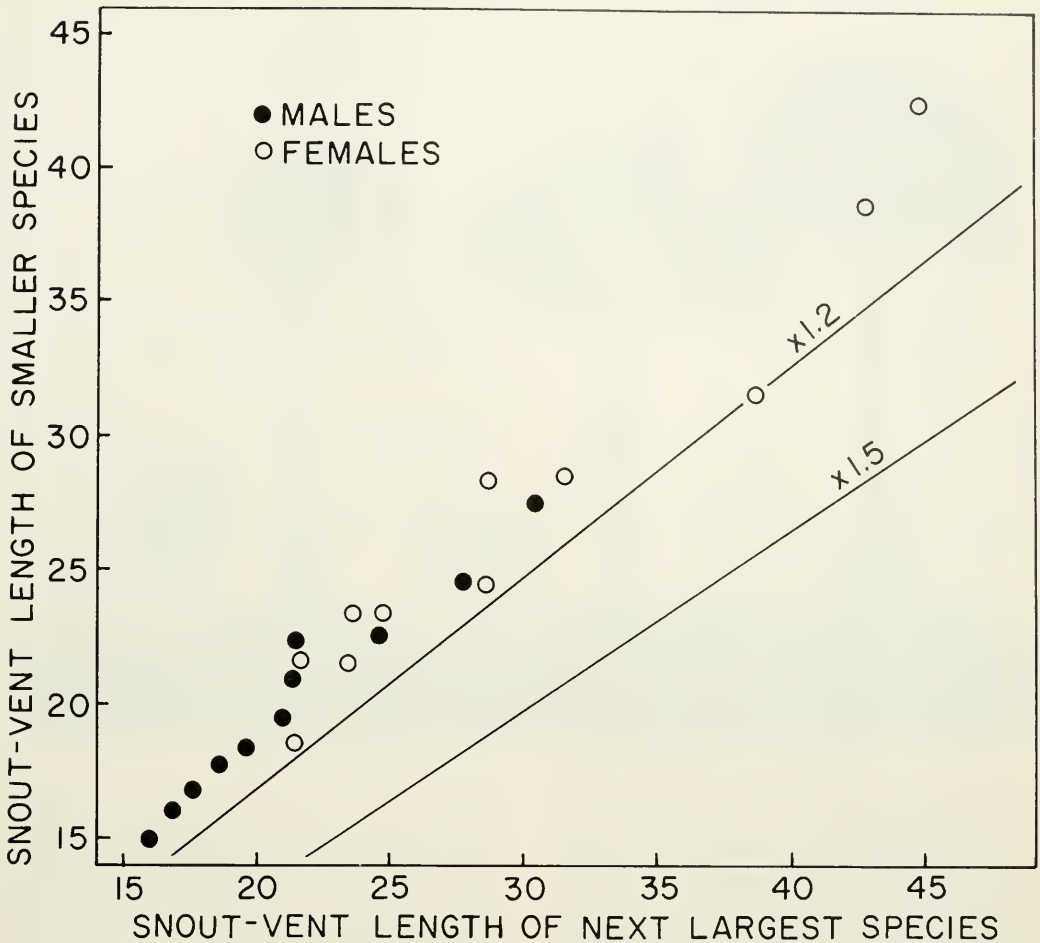


FIG. 182.—Ratios of body lengths of succeeding larger nocturnal arboreal species of *Eleutherodactylus* in primary forest. The lines delimit the ratios of 1.2-1.5 suggested by Hutchinson (1958).

pling. Among the 26 species in this assemblage (18 frogs, 7 snakes, 1 lizard), three species were not in the bush-inhabiting subcommunity; these are: 1) the only nocturnal lizard, *Thecadactylus rapicauda*, which feeds on large arthropods, mostly roaches, on trunks and limbs of large trees; 2) the hylid frog *Nyctimantis rugiceps*, feeding entirely on orthopterans and inhabiting cavities in trees and large bamboo; and 3) the boid snake *Corallus caninus*, which feeds on small arboreal mammals.

Most taxonomic groups inhabiting the primary forest are either terrestrial or

arboreal. Some *Eleutherodactylus* are active on the ground, but most are arboreal. The six species of *Anolis* provide a notable exception and occur from the ground to the canopy (Fig. 183). *Anolis transversalis* occurs exclusively in the trees, whereas *A. punctatus* occurs in trees and bushes. Examples of both species have been obtained from the same tree. *Anolis fuscoauratus* and *A. trachyderma* forage in low bushes and on the ground, and *A. ortonii* inhabits the bases of trees and forages on the surrounding ground. *Anolis chrysolepis* is strictly terrestrial. The most common

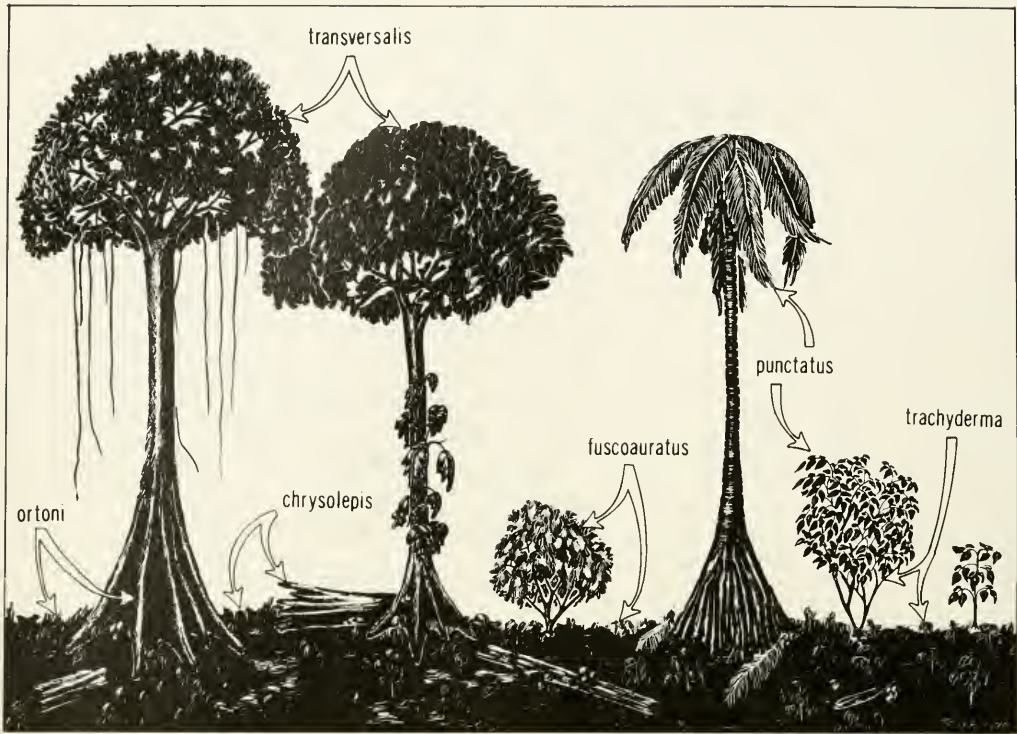


FIG. 183.—Microhabitats of six species of *Anolis* in primary forest.

prey items of the six species include four groups of arthropods (Table 25). These data and the niche overlap values (Table 23) show that among the species of *Anolis*, *fuscoauratus* and *trachyderma* are more nearly alike than are the others. Comparisons of sites of capture and relative numbers of individuals (see account of *A. trachyderma* for data) suggest that *A. trachyderma* is more abundant in secondary forest than is *A. fuscoauratus*; perhaps the latter is less tolerant of sunlight and more susceptible to desiccation than is *A. trachyderma*. Thus, their pri-

mary foraging zones might be different but probably overlap broadly; both species have been observed in the same bush and foraging within a meter of one another on the ground.

Secondary Forest

As noted previously, most of the 118 species known to occur in secondary forest also inhabit primary forest. Of those species that have been collected only in secondary forest, the following are represented by no more than three specimens each: *Bolitoglossa equatori-*

TABLE 25.—Comparative Major Dietary Items (by volume) in *Anolis*.

SPECIES	N	FOOD	
		Primary	Secondary
<i>A. chrysolepis</i>	25	Orthoptera (28%)	Coleoptera (16%)
<i>A. fuscoauratus</i>	25	Orthoptera (25%)	Arachnida (24%)
<i>A. ortonii</i>	7	Formicidae (54%)	Orthoptera (21%)
<i>A. punctatus</i>	14	Orthoptera (36%)	Formicidae (29%)
<i>A. trachyderma</i>	27	Arachnida (42%)	Orthoptera (10%)
<i>A. transversalis</i>	3	Coleoptera (100%)	

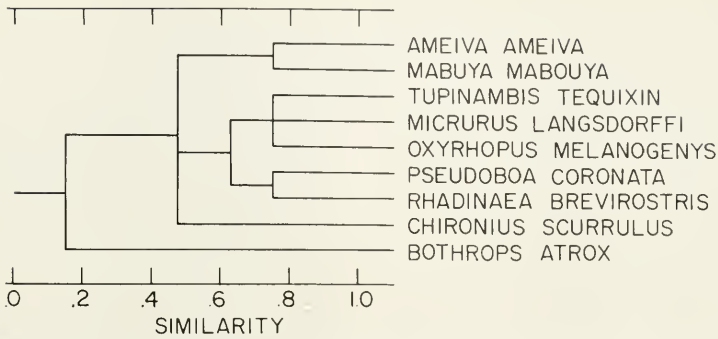


FIG. 184.—Modal resource utilization by diurnal reptiles in clearings based on size, substrate, and food.

ana, *Ceratophrys cornuta*, *Leptodactylus stenodema*, and *Corallus enydris*. The scant amount of data on these species does not preclude their existence in primary forest.

Of the remaining six species apparently confined to secondary forests, four are small bush-dwelling species of *Hyla* (*brevifrons*, *cruentomma*, *rhodopepla*, and *riveroi*) that breed in ephemeral ponds. The very abundant, small *Eleutherodactylus variabilis* also is a bush inhabitant. The last species is a bush-dwelling snake, *Imantodes lentiferus*.

All of the species apparently confined to secondary forest are nocturnal. Only *Ceratophrys cornuta* and *Leptodactylus stenodema* are terrestrial. *Ceratophrys* is a large predatory species, consuming large arthropods, frogs, and small mammals; the salamander and the other frogs eat small arthropods. *Corallus enydris* and *Imantodes lentiferus* eat frogs.

Clearings

By comparison with the fauna in the forests, the subcommunity inhabiting clearings is small (24 species) and relatively simple to analyze. Although some of the nocturnal frogs do perch on bushes and herbs, all species are considered to be terrestrial. They are readily identified into two assemblages – diurnal (9 species) and nocturnal (16 species); *Bothrops atrox* is a member of both assemblages (Figs. 184-185). Four am-

phibians (*Bufo glaberrimus*, *B. marinus*, *Hyla rubra*, and *H. triangulum*), two lizards (*Ameiva ameiva* and *Mabuya mabouya*), and seven snakes (*Clelia clelia*, *Drepanoides anomalus*, *Liophis cobella*, *Micrurus langsdorffi*, *Oxyrhopus melanogenys*, *Pseudoboa coronata*, and *Siphlophis cervinus*) apparently are restricted to clearings.

Of all the assemblages analyzed, the diurnal group in clearings is unique in the absence of anurans (Fig. 184). This assemblage consists of three lizards and six snakes. All of the lizards are heliophilous; *Ameiva* and *Mabuya* prey on a variety of arthropods and *Tupinambis* is omnivorous. The diet of *Micrurus langsdorffi* is unknown, but if it is like other terrestrial *Micrurus* it feeds on snakes and lizards. *Chironius fuscus* ferrets frogs out of their diurnal retreats, and the other snakes feed on lizards; *Bothrops atrox* also eats frogs and mammals, both of which it probably captures at night.

In the nocturnal assemblage, there are nine frogs and seven snakes (Fig. 185). The frogs contain three ubiquitous species (*Bufo marinus*, *Hyla lanciformis* and *Hyla rubra*) that usually can be observed on any night of the year. The five species of *Hyla* and *Leptodactylus mystaceus* congregate at ephemeral ponds, whereas the *Bufo* and *Leptodactylus wagneri* are scattered throughout the clearings. All of the anurans feed on

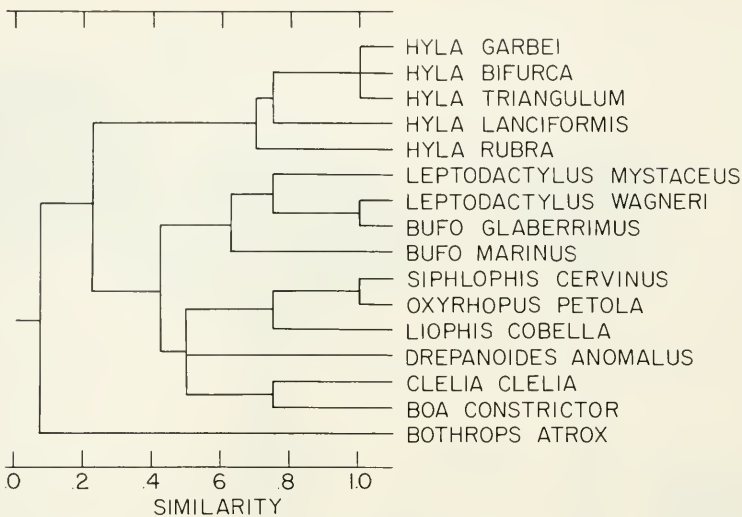


FIG. 185.—Modal resource utilization by nocturnal amphibians and reptiles in clearings, based on size, substrate, and food.

a wide variety of arthropods. Of the snakes, only *Liophis* is restricted to frogs, *Bothrops*, *Boa*, and *Clelia* feed on small mammals and lizards; the former also eats frogs and the latter snakes. *Oxyrhopus petola* and *Siphlophis* apparently seek out lizards in their nocturnal retreats. One *Clelia* was eating an *Ameiva* when captured at night. According to Bailey (1966:68), *Drepanoides* eats reptile eggs.

DIEL ACTIVITY

The herpetological community at Santa Cecilia contains more nocturnal than diurnal species (Table 26); most of the anurans are nocturnal, but only one (*Thecadactylus rapicauda*) of 30 lizards is nocturnal. The strictly diurnal anurans occur in the forest and consist of all six species of dendrobatids, two bufonids (*Bufo typhonius* and *Dendrophryniscus minutus*), and three leptodactylids (*Eda-*

lorhina perezii, *Eleutherodactylus nigrovittatus* and *E. sulcatus*). Eight other anurans are active both at night (ground or low vegetation) and by day (ground); these include the hylid *Hemiphractus proboscideus* and seven leptodactylids (*Eleutherodactylus conspicillatus*, *E. croceinguinis*, *E. lanthanites*, *E. ockendeni*, *Leptodactylus discodactylus*, *Lithodytes lineatus*, and *Adenomera andreae*). The three snakes that are active by day and night include the terrestrial *Bothrops atrox*, the forest-dwelling *Epicrates cenchria*, and the aquatic *Helicops angulatus*.

Analysis of habitat and vertical distribution with respect to diel activity reveals that most terrestrial species are diurnal, whereas most arboreal species are nocturnal (Table 27). The iguanid lizards are a major exception to this generality; all iguanids are diurnal, and nine

TABLE 26.—Diel Activity of Taxonomic Groups in the Herpetofauna.

GROUP	Diurnal	Nocturnal	Both
Salamanders	0 (0%)	2 (100%)	0 (0%)
Anurans	11 (13%)	68 (78%)	8 (9%)
Lizards	29 (97%)	1 (3%)	0 (0%)
Snakes	26 (49%)	24 (45%)	3 (6%)
TOTALS	66 (39%)	95 (55%)	11 (6%)

TABLE 27.—Diel Activity in Relation to Habitat and Vertical Distribution.
(Numbers are amphibians/reptiles.)

HABITAT	Diurnal		Nocturnal	
	Arboreal	Terrestrial	Arboreal	Terrestrial
Secondary Forest	4/12	16/40	49/11	16/8
Primary Forest	3/8	12/32	53/12	15/8
Clearings	0/0	0/9	5/0	4/7

of the 11 species are at least partly arboreal.

Some diurnal terrestrial species sleep at night on herbs or bushes. The anurans *Dendrobates* (3 species), *Dendrophryniscus*, and *Bufo typhonius* usually sleep on leaves of herbs < 0.5 m above the ground, but the *Bufo* sometimes utilize perches > 1 m. Many of the racer-like snakes (*Chironius*, *Dendrophidion*, *Drymoluber*) sleep on bushes and low trees 1-3 m above the ground.

All diurnal amphibians shun sunlight; thus, they are present only in the forest. Eighteen of the 29 diurnal lizards live in deep shade. This group includes all of the gekkonids, and *Anolis*, and most of the microteiids. Other terrestrial species in the forest are active in patches of sunlight; these include *Kentropyx*, *Leposoma*, *Prionodactylus manicatus*, and *Enyalioides cofanorum*, plus *Plica umbra*, which also basks on tree trunks. *Enyalioides laticeps*, and *Polychrus marmoratus* are arboreal heliophiles. The large teiids *Dracaena* and *Tupinambis* are active in direct sunlight, but they also seek shade at warmer times of the day. The most conspicuously heliophilous species are *Ameiva ameiva* and *Mabuya mabouya*; both are active only in sunlight. No individuals of either of these common species were observed during one period of 30 days of heavy cloud cover.

Fitch (1968) reported on body temperatures of some lizards at Santa Cecilia. Mean body temperatures for four heliophilous species (*Ameiva*, *Kentropyx*, *Mabuya*, and *Prionodactylus manicatus*) were 29.7-37.0 ($\bar{x}$ =34.31)°C; temperatures for five sciophilous species (*Neusticurus*, *Gonatodes*, *Iphisa*, *Priono-*

dactylus argulus, and *Anolis chrysolepis*) were 26.8-30.1 ($\bar{x}$ =28.3)°C. Although these data are limited to a small sample of species, it is obvious that the species that are active in the shade have lower optimal temperature requirements than do the heliophilous species.

In contrast to the lizards, most diurnal snakes are heliophiles; at least most individuals have been found in sunny situations. The optimal time for finding diurnal snakes is mid-morning on a sunny day. Mid-day temperatures (sunny days) apparently are excessive for most species. Only four diurnal snakes are known to be sciophilous; these are *Atractus occipitoalbus*, *Leptomicrurus narducci*, *Tantilla melanocephala*, and *Xenopholis scalaris*.

Activity of nocturnal species is negatively correlated with moonlight. On nights with three-quarter to full moon there is relatively little anuran and snake activity, even though it may be raining and have a moderate amount of cloud cover. Abundant species of frogs, such as *Hyla lanciformis* and *H. rubra*, which begin calling nightly at dusk, sometimes cease calling in about half an hour on moonlit nights, whereas on dark nights they may call throughout the night.

DIET AND FEEDING

With a few exceptions, amphibians and lizards have generalized diets consisting of a wide array of arthropods. These insectivorous animals are all essentially secondary consumers (tertiary when the diet consists of spiders). They prey on any insect (except distasteful ones) that they can capture. Prey size is a limiting factor in that many tropical

insects, especially orthopterans and coleopterans are too large to be captured, let alone ingested, by many small species of amphibians and lizards. On the other hand, larger species frequently consume many kinds of small prey. Thus, in these generalists, size of the predator is positively correlated with the maximum, but not the minimum, size of the prey.

Among the frogs obligate feeding on ants occurs in two species of microhylid frogs (*Chiasmocleis anatipes* and *C. ventrimaculata*), two hylids (*Sphaenorhynchus carneus* and *S. eurhustus*) and in *Dendrobates quinquevittatus*. Ants also form the majority of the diet in *Chiasmocleis bassleri*, *Hamptophryne boliviana*, and *Eleutherodactylus acuminatus*. All of these frogs are small (maximum snout-vent lengths of 14.0-39.0 in males and 16.0-48.0 in females) and, with the exception of *Dendrobates quinquevittatus*, have pointed snouts. The small *Physalaemus petersi* feeds only on termites.

Two frogs are specialized for consuming large prey; *Ceratophrys cornuta* and *Hemiphractus proboscideus* have relatively huge heads and large gapes. These "hopping stomachs" are capable of ingesting prey nearly equal to their own bulk; both eat frogs and large orthopterans, and *Ceratophrys* also eats small mammals.

Only two lizards are obligate in their diets. *Plica umbra* feeds exclusively on ants, and *Dracaena guianensis* eats snails. The large teiid, *Tupinambis tequixín*, is omnivorous, feeding on insects, small mammals, bird eggs, and vegetation. No other species of lizard at Santa Cecilia is herbivorous.

Partial analyses of major dietary items and niche overlap in food for some ecological groups (guilds) of amphibians and reptiles are presented in tables 19-25. The lizards were chosen as an example of niche breadth analysis using Simpson's index of diversity for niche breadth (Colwell and Futuyma, 1971: 568; Pianka, 1972:59). Prey items from

526 lizards of 27 species were identified in 19 categories. Niche overlap values range from 0.00 to 0.86, whereas niche breadth scores are 1.00 to 18.91 (standardized scores = 0.053-0.995) (Table 28). Two hundred seventy-seven (85%) of the 325 potential overlaps are realized ($C_{ij} > 0.0$) along the food dimension.

Thirteen of the 27 species have overlap values of 30-40 percent; none is more than 40 percent, and only four species are below 10 percent. Only two species have standardized niche breadth scores of more than 0.5 (*Gonatodes concinna* 0.516, *Ameiva ameiva* 0.995).

In contrast to anurans and lizards, snakes are more specialized in their feeding, although juveniles may feed on different kinds of prey than the adults. Dentional modifications can be correlated with specialized feeding in diverse taxa of snakes (Anthony, 1955; Edmund, 1969). Most snakes feed on vertebrates, but three feed exclusively on earthworms, three on arboreal snails, and one on centipedes. Frogs are eaten by 16 species, lizards by 14, and mammals by six. Another six food categories are distributed as follows: birds 1, snakes, 4, reptile eggs 1, tadpoles 1, caecilians 1, and fish 2.

These data are more meaningful when viewed with respect to structural habitat and diel activity of the snakes (Table 29). Thus, there is differential utilization of food resources at different times and in different structural habitats.

SIZE RATIOS

Hutchinson (1959) and Schoener (1965) noted progressive increases in size of trophic appendage ratios for mammals and birds. The sizes of the trophic appendages are positively correlated with body size in lizards of the genus *Anolis* (Schoener, 1967) and in hylid frogs (Caldwell, 1973); thus, body size ratios can be used in these groups to determine if a regular progression of body size or "biological constant"

(Schoener, 1970) exists among sympatric associations of these groups.

Schoener (1965, 1969, 1970) discovered that body size ratios in insectivorous birds and anoline lizards on West Indian islands show a regular progression of size within a community. Generally, larger ratios occurred among larger species and smaller ratios among smaller species. Schoener (1965) suggested that this pattern may be due to the uneven distribution of the biomass of insects upon which the birds were feeding. Caldwell (1973) found similar patterns in communities of tree frogs and concluded that food probably is the most important factor influencing body size in tree frog communities.

Size ratios of anurans and lizards at Santa Cecilia were calculated from the mean snout-vent lengths of the 10 largest individuals of each sex (fewer if there were less than 10 adults). The studies by Caldwell and Schoener (*supra cit.*) each dealt with one congeneric assemblage of species. The ratios generally ranged from 1.2 between smaller species to 1.5 between larger species. The ratios among the six species of *Anolis* at Santa Cecilia are 1.02-1.46 in males and 1.01-1.30 in females, but the species are not in the same size order in males and females (Table 30). Similar discrepancies are found in ratios of body size in frogs inhabiting the forest floor by day (Table 21) and in nocturnal arboreal species of *Eleutherodactylus* (Fig. 182). In fact no grouping, either taxonomic or ecological, yields the results anticipated from conclusions of Hutchinson, Schoener, and Caldwell.

TADPOLES

Larval amphibians have a completely different suite of ecological requirements than do the adults; consequently they are subject to entirely different selective pressures. No detailed ecological studies of tadpoles were undertaken, but some general observations indicate tadpoles occur into different ecological situations.

Wilbur (1972) demonstrated experimentally several factors significant to the coexistence of small communities. Structural differences (principally in the caudal fins and mouth) among tadpoles are adaptations for locomotion and feeding in different situations. For example, high dorsal fins and anteroventral mouths are characteristic of midwater grazers, and moderate dorsal fins and anterior mouths are characteristic of pelagic filter feeders, whereas low caudal fins and ventral mouths are characteristic of bottom grazers.

The pond-dwelling tadpoles at Santa Cecilia have been grouped into three categories: vegetation-choked areas, pelagic, and bottom-dwellers. No more than 10 species of tadpoles were found in any one pond at one time. At a forest pond, the numbers of species of tadpoles inhabiting vegetation-choked areas, pelagic situations, and bottom were 2-7-1. At a forest-edge pond the numbers were 3-4-1, and at a pond in a clearing they were 7-2-1.

I suspect that analysis of gut contents of tadpoles combined with more refined ecological analysis will demonstrate that the numerous species of tadpoles inhabiting forest utilize different resources in their coexistence in restricted habitats. Heyer (1976) suggested that interspecific competition is non-existent among tadpoles.

There are few species of stream-inhabiting tadpoles at Santa Cecilia; tadpoles of *Centrolenella* live under cover on the bottoms of streams, whereas tadpoles of dendrobatids graze on algae on rocks. Tadpoles of three species are unique in their habits. The tadpoles of *Hyla geographica* occur in large schools in lakes. Those of *Hyla boans* develop in shallow nests at the edges of rivers. The carnivorous tadpoles of *Ceratophrys cornuta* inhabit shallow ponds where they prey on tadpoles. Tadpoles of *Nyctimantis rugiceps* and of the species of *Dendrobates* develop in constrained bodies of water (tree holes, bases of palm

TABLE 28.—Niche Overlap Values and Niche Breadth Scores
in Lizards and Amphisbaenians for prey eaten.

SPECIES	N	<i>Gonatodes concinnatus</i> (A)	<i>Pseudogonatodes quianensis</i> (B)	<i>Thecadactylus rapicauda</i> (C)	<i>Anolis chrysolepis</i> (D)	<i>Anolis fuscoauratus</i> (E)	<i>Anolis ortonii</i> (F)	<i>Anolis punctatus</i> (G)	<i>Anolis trachyderma</i> (H)	<i>Anolis transversalis</i> (I)	<i>Enyalioides cofanorum</i> (J)	<i>Enyalioides laticeps</i> (K)	<i>Plica umbra</i> (L)	<i>Polychrus marmoratus</i> (M)
A	10													
B	11	.50												
C	7	.36	.30											
D	26	.62	.34	.32										
E	25	.53	.47	.36	.68									
F	7	.37	.30	.21	.34	.41								
G	14	.43	.29	.26	.54	.54	.47							
H	27	.61	.31	.30	.57	.65	.31	.28						
I	3	.07	.15	.18	.33	.24	.11	.24	.09					
J	6	.36	.43	.27	.36	.46	.22	.37	.42	.14				
K	24	.50	.30	.39	.35	.43	.22	.34	.62	.04	.28			
L	11	.07	.08	.00	.04	.14	.56	.28	.00	.00	.00	.00		
M	6	.15	.19	.18	.29	.31	.11	.33	.15	.86	.28	.10	.00	
N	1	.07	.00	.00	.07	.07	.00	.22	.06	.00	.29	.07	.00	.14
O	29	.56	.41	.48	.52	.55	.36	.57	.43	.57	.39	.47	.06	.49
P	10	.56	.42	.38	.26	.31	.25	.22	.52	.07	.28	.54	.00	.07
Q	106	.60	.29	.32	.63	.51	.30	.52	.55	.20	.32	.52	.02	.27
R	6	.43	.15	.14	.26	.21	.27	.22	.21	.00	.28	.16	.00	.14
S	11	.08	.28	.09	.07	.03	.00	.00	.06	.00	.14	.23	.00	.00
T	1	.14	.00	.45	.04	.00	.00	.06	.03	.00	.00	.07	.00	.00
U	84	.51	.33	.54	.54	.66	.29	.44	.51	.40	.31	.36	.00	.40
V	38	.61	.38	.18	.45	.47	.42	.43	.36	.07	.21	.30	.23	.07
W	25	.58	.58	.49	.50	.66	.38	.40	.55	.13	.45	.52	.13	.19
X	20	.68	.37	.42	.43	.52	.41	.25	.68	.07	.25	.58	.04	.07
Y	11	.48	.31	.49	.45	.58	.33	.35	.61	.20	.29	.48	.00	.20
Z	1	.20	.07	.18	.29	.24	.11	.39	.15	.50	.14	.23	.00	.14
AA	3	.07	.08	.10	.05	.16	.36	.28	.00	.00	.14	.08	.33	.00
$\bar{x}C_{ih}$		.393	.282	.284	.344	.391	.278	.333	.347	.180	.291	.317	.076	.198
B		9.80	5.46	2.69	5.32	5.50	2.80	4.44	5.36	1.00	4.00	4.56	1.00	1.32
B _{ST}		.516	.287	.142	.280	.289	.147	.234	.282	.053	.211	.240	.053	.070

<i>Uracentron flaviceps</i> (N)	<i>Mabuja mabouya</i> (O)	<i>Alopoglossus copii</i> (P)	<i>Ameiva ameiva</i> (Q)	<i>Arthrosaura reticulata</i> (R)	<i>Bachia trinasale</i> (S)	<i>Iplisa elegans</i> (T)	<i>Kentropyx peliceps</i> (U)	<i>Leposoma parietale</i> (V)	<i>Neusticurus ecleopus</i> (W)	<i>Prionodactylus argulus</i> (X)	<i>Prionodactylus manicatus</i> (Y)	<i>Tupinambis teguixin</i> (Z)	<i>Amphisbaena fuliginosa</i> (AA)
.06													
.00	.45												
.07	.54	.33											
.14	.25	.27	.27										
.00	.04	.00	.04	.00									
.00	.10	.13	.05	.14	.00								
.01	.70	.42	.46	.28	.00	.16							
.00	.31	.26	.44	.28	.10	.06	.36						
.06	.57	.55	.40	.22	.18	.16	.53	.47					
.00	.45	.66	.42	.36	.06	.18	.59	.51	.58				
.00	.49	.66	.42	.26	.01	.13	.68	.32	.48	.72			
.00	.49	.14	.39	.00	.00	.00	.40	.06	.12	.06	.20		
.00	.11	.01	.03	.01	.42	.01	.00	.23	.16	.04	.01	.01	
.050	.397	.300	.340	.190	.070	.073	.380	.290	.400	.360	.352	.158	.010
1.00	4.23	3.69	18.91	4.45	2.28	1.00	3.77	6.33	7.01	4.40	2.78	2.00	3.00
.053	.223	.194	.995	.234	.120	.053	.198	.333	.369	.237	.146	.105	.158

TABLE 29.—Prey of Snakes in Relation to Habitat.
(Numbers are diurnal/nocturnal species of snakes.)

PREY	Terrestrial	Arboreal	Aquatic	Total
Earthworms	3/0	0/0	0/0	3/0
Snails	0/0	0/3	0/0	0/3
Centipedes	1/0	0/0	0/0	1/0
Fish	0/0	0/0	1/1	1/1
Caecilians	1/0	0/0	0/0	1/0
Tadpoles	1/0	0/0	0/1	1/1
Frogs	8/5	3/8	0/0	11/13
Lizards	5/8	2/3	0/0	7/11
Snakes	3/1	0/0	0/0	3/1
Reptile Eggs	0/1	0/0	0/0	0/1
Birds	0/0	0/1	0/0	0/1
Mammals	2/2	1/2	1/1	4/5
TOTAL	24/17	6/17	2/3	32/37

TABLE 30.—Size Ratios in Sympatric Species of *Anolis*.

MALES	$\bar{x}$ SVL	Ratio	FEMALES	$\bar{x}$ SVL	Ratio
<i>A. punctatus</i>	79.0		<i>A. chrysolepis</i>	78.8	
<i>A. chrysolepis</i>	75.8	1.04	<i>A. transversalis</i>	72.0	1.09
<i>A. transversalis</i>	71.5	1.06	<i>A. punctatus</i>	71.5	1.01
<i>A. trachyderma</i>	48.9	1.46	<i>A. trachyderma</i>	54.8	1.30
<i>A. ortonii</i>	44.4	1.10	<i>A. fuscoauratus</i>	46.8	1.17
<i>A. fuscoauratus</i>	43.4	1.02	<i>A. ortonii</i>	42.5	1.10

fronds, bromeliads); those of at least some species of *Dendrobates* are cannibalistic.

ANURAN MATING CALLS

In addition to the differential utilization of the physical and biotic resources in the environment, most anurans have another dimension in which they exhibit differences. Each species has a characteristic mating call that differs from the calls of other syntopic species. Fouquette (1960) demonstrated the importance of the mating call as a pre-mating isolating mechanism, and Duellman (1967) elaborated on the mating call and other courtship isolating mechanisms in ten sympatric hylids in Costa Rica.

Presumably differences in mating calls are most essential in multi-species breeding congregations, such as common to many species of hylids. Accordingly, data obtained from recordings of 1-10 individuals of 20 species of pond-breeding hylids at Santa Cecilia were subjected to stepwise discriminant analysis.

Seven variables were used: 1) number of notes in call group, 2) note repetition rate, 3) number of secondary notes, 4) duration of note, 5) pulse rate, 6) fundamental frequency, 7) dominant frequency (see Duellman, 1970b for definitions).

In the first analysis two questions were posed: Can the 20 species be distinguished on the basis of the call parameters used? Which character(s) are most important in discriminating between species? Examination of the correlation matrix reveals that of the seven parameters, only numbers 6 (fundamental frequency) and 7 (dominant frequency) are highly correlated ($r=0.903$). Variable six is the best discriminator, followed by variables seven, five, and three. At this point the model discriminates 96 percent of the individuals. The multivariate means of the 20 species are shown in a three dimensional plot (Fig. 186), in which canonical axis I subsumes 62 percent of the dispersion in the multivariate data cloud; axis II subsumes

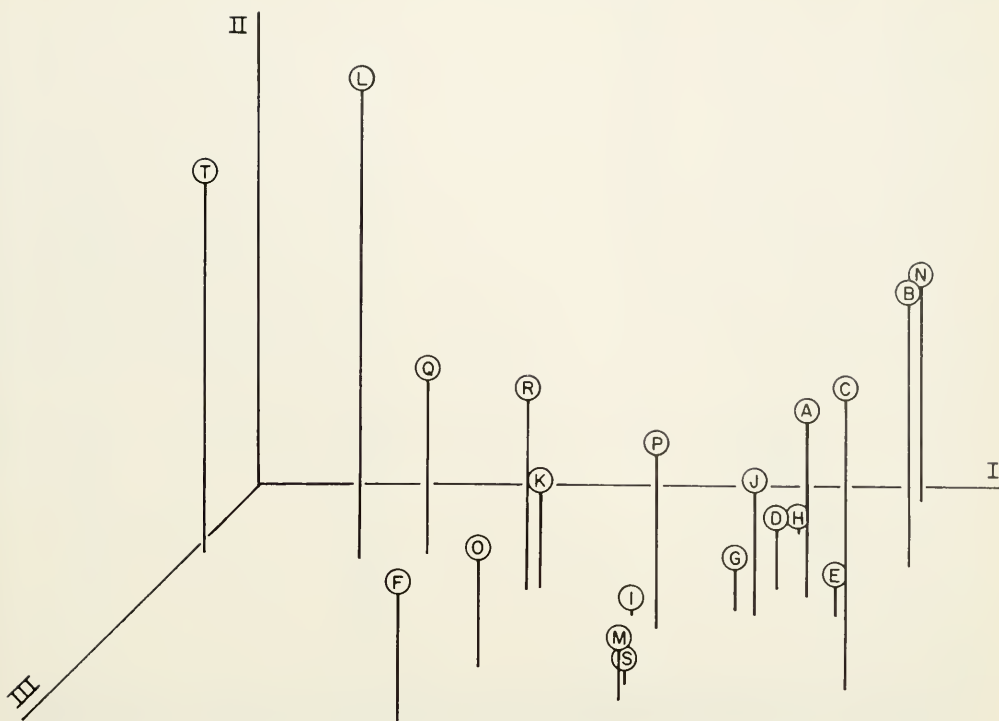


FIG. 186.—Three dimensional plot of the multivariate means of call parameters of 20 species of pond-breeding hylid frogs (see text for explanation of the canonical axes). A. *Hyla bifurca*, B. *H. bokermanni*, C. *H. brevifrons*, D. *H. calcarata*, E. *H. cruentomma*, F. *H. garbei*, G. *H. geographica*, H. *H. granosa*, I. *H. lanciformis*, J. *H. leucophyllata*, K. *H. marmorata*, L. *H. parviceps*, M. *H. punctata*, N. *H. rhodopepla*, O. *H. rubra*, P. *H. sarayacuensis*, Q. *H. triangulum*, R. *Phyllomedusa palliata*, S. *P. tarsius*, T. *Sphaenorhynchus carneus*.

about 20 percent, and axis III about 8 percent. In general, the species are well sorted, but some are quite similar to one another.

If only sympatric and synchronously breeding species are analysed together, similar broad sorting occurs but the species that closely approximated one another in figure 186 are in separate breeding congregations (Figs. 187-190). Thus, within given breeding congregations each species tends to have an individual acoustical niche.

NICHE DIMENSIONS

Ideally, the realized niche for each of the species in the community could be assessed by measuring numerous dimensions (resources utilized); comparisons of the dimensions for each species

would provide a picture of the ecological relationships of the members of the community. The ideal approach is not feasible for the entire community; too few data are available on snakes to provide a meaningful analysis. An overall analysis of the anurans likewise has little merit, because data on many of the species only reflect certain parameters when the animals are in breeding congregations. The data on lizards are the most suitable for multidimensional analysis.

Ecological data on 1506 specimens of 28 lizards and one amphisbaenian were analyzed with respect to four dimensions of the niche: habitat (13 categories), substrate (9), microhabitat (5), and prey (19). 8 Diel activity was not included in the analysis; all of the lizards, except *Thecadactylus rapicauda*, are di-

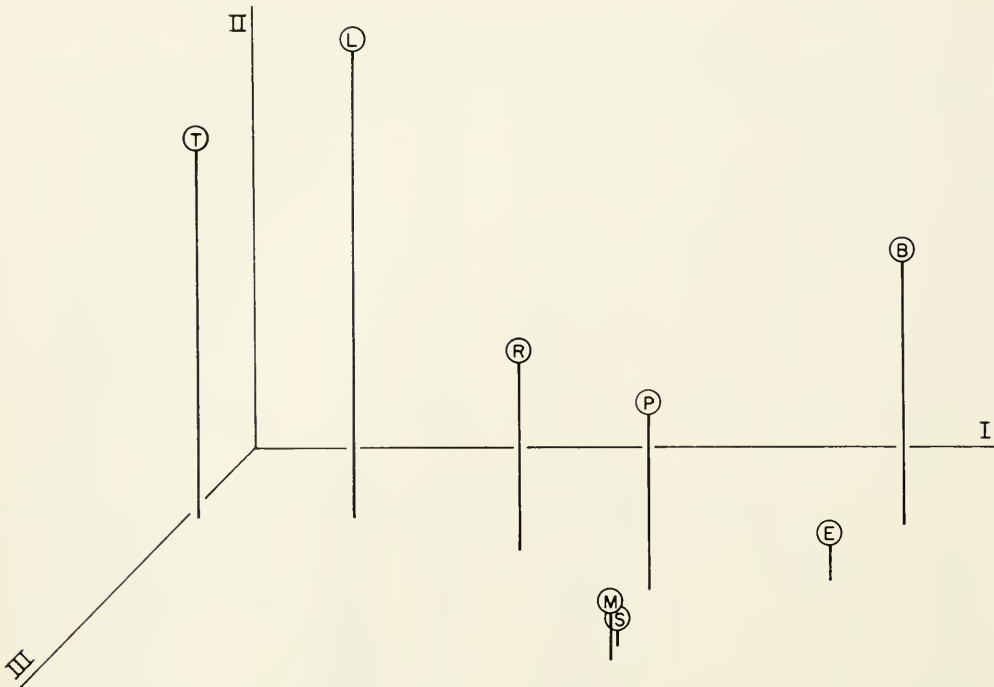


FIG. 187.—Three dimensional plot of the multivariate means of call parameters of eight species of hylid frogs in a breeding aggregation at a pond in primary forest (Letters refer to species listed in legend to figure 186).

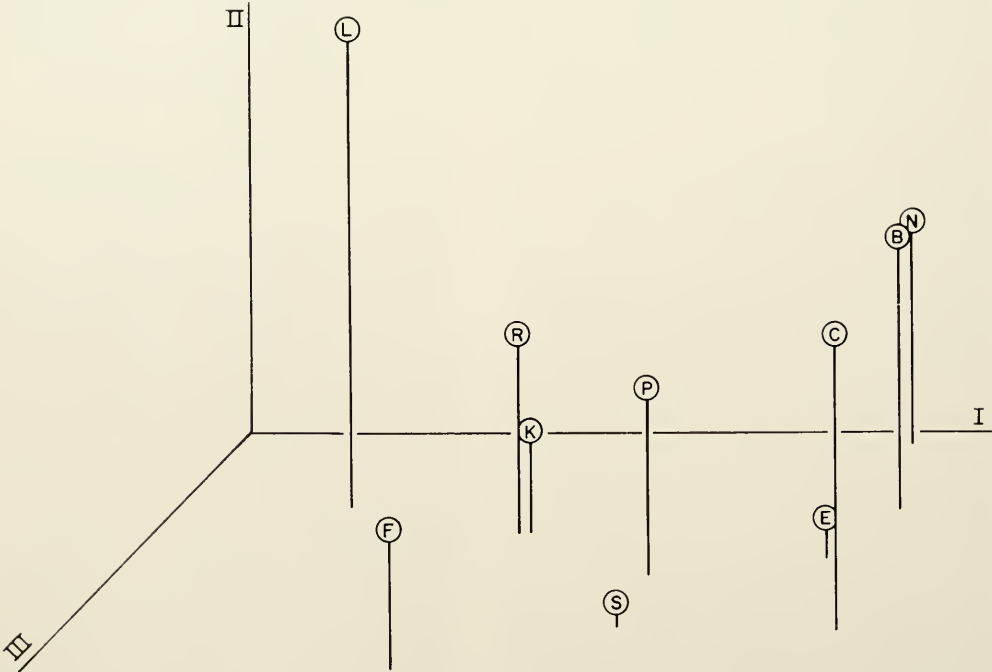


FIG. 188.—Three dimensional plot of the multivariate means of call parameters of ten species of hylid frogs in a breeding aggregation at a pond in secondary forest (Letters refer to species listed in legend to figure 186).

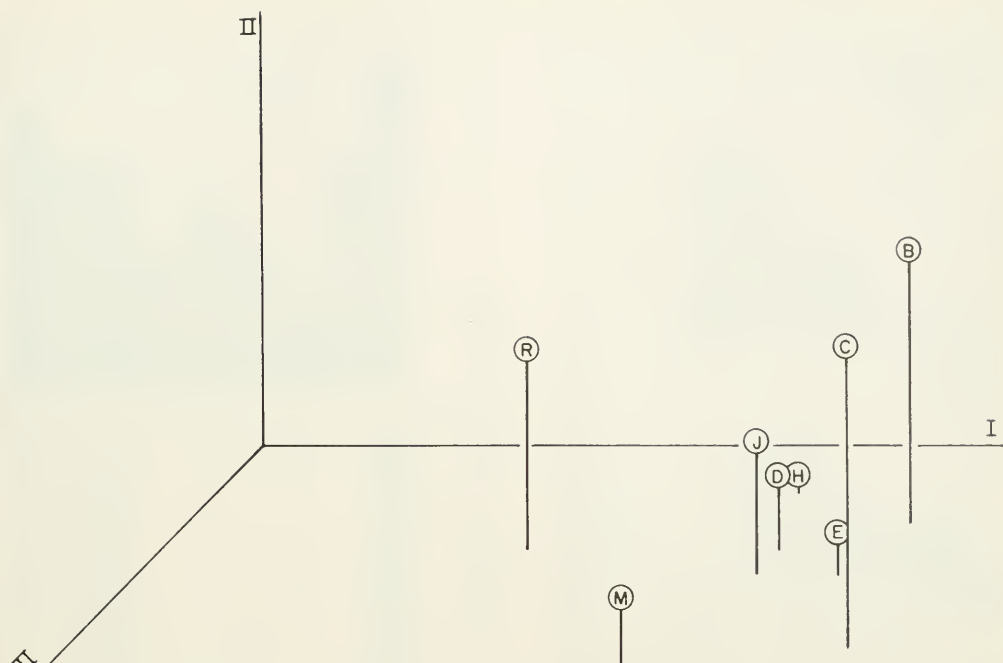


FIG. 189.—Three dimensional plot of the multivariate means of call parameters of eight species of hyliid frogs in a breeding aggregation at a forest-edge pond (Letters refer to species listed in legend for figure 186).

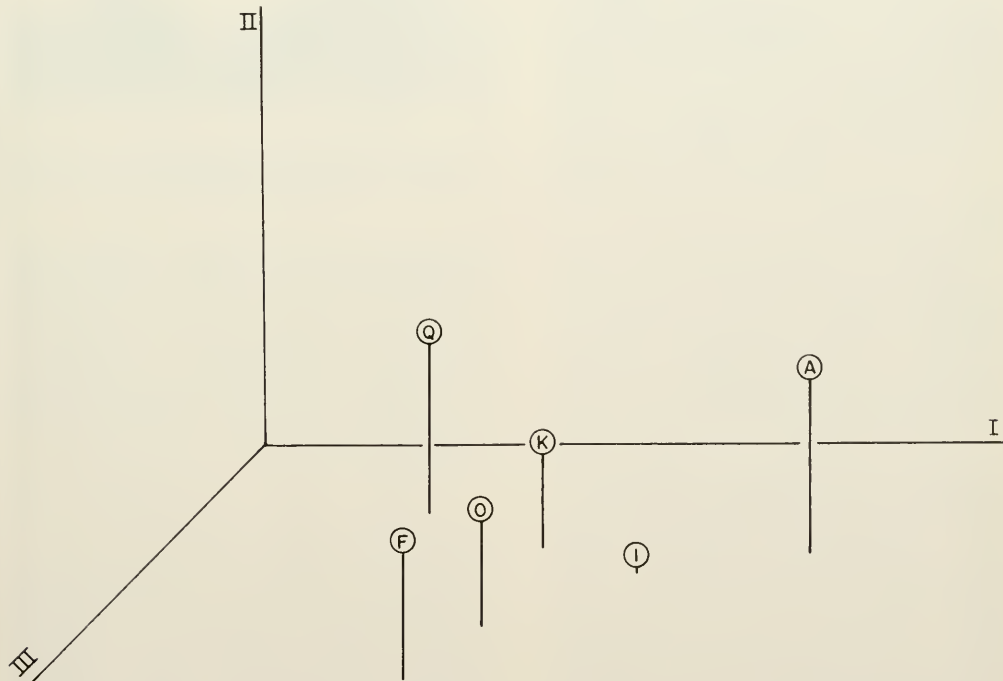


FIG. 190.—Three dimensional plot of the multivariate means of call parameters of six species of hyliid frogs in a breeding aggregation at a pond in a clearing (Letters refer to species listed in legend to figure 186).

urnal. No *Polychrus marmoratus* were found while active (all were sleeping at night), so that species was omitted from the analysis.

The proportions of individuals of each species associated with each category provided the basis for quantifying the niche breadth (B) along each dimension using Simpson's index of diversity (Colwell and Futuyma, 1971). In order to compare niche breadths along different dimensions, each niche value was standardized (B_{ST}) by dividing the value by the number of categories in that particular dimension. The overall niche breadth (4-dimensional) was calculated as the mean of the four standardized niche breadths ($\Sigma B_{ST}/4$). Niche overlaps values (C_{ih}) were computed using the formula proposed by Colwell and Futuyma, 1971). Overall niche overlap was computed by multiplying for each pair the four overlap values and the total $\times 100$. In this method overall niche overlap is 0 if overlap along any one dimension is 0.

Frequency distributions of niche overlaps for each dimension are given in figures 191-192; frequency distributions of standardized niche breadths, numbers of overlaps in four dimensions, and mean niche overlap values are shown in figure 193. Various niche overlap values are given in Table 31.

From these analyses certain features are evident. Mean niche breadth is a function of sample size ($r=0.42$, $0.05 > P > 0.01$). This correlation could be a reflection of sampling bias in the estimates of niche breadth, or it could mean that the more common species have broader niches (which is why they are common), or it could be a combination of the two. There is no correlation between mean overlap values and mean standardized niche breadth ($r=-0.016$). There is a highly significant correlation ($r=0.62$, $P < 0.01$) between mean niche breadth and the number of overlaps in 4-space. Thus, lizards with broad niches tend to overlap with more

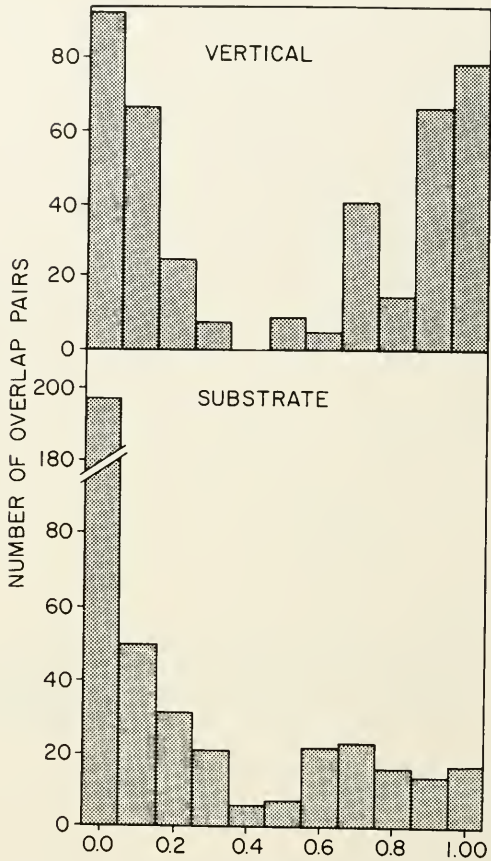


FIG. 191.—Number of overlap pairs among 29 species of lizards with respect to vertical distribution and substrate.

species than do species with narrow niches, but they do not necessarily share more overlap space. Of the six possible comparisons among four niche dimensions, only habitat-substrate is significant ($r=0.698$, $P < 0.01$); thus, lizards with broad habitats also have broad substrate utilization.

Relative positions of all species along a standardized niche breadth continuum are shown in Figure 194. Forest inhabitants (those species for which 50 percent or more of the specimens were taken in primary forests) tend to have narrower niches ($\bar{X} B_{ST}=0.232$) than on-forest species ($\bar{X} B_{ST}=0.190$), but the differences are not statistically significant. The

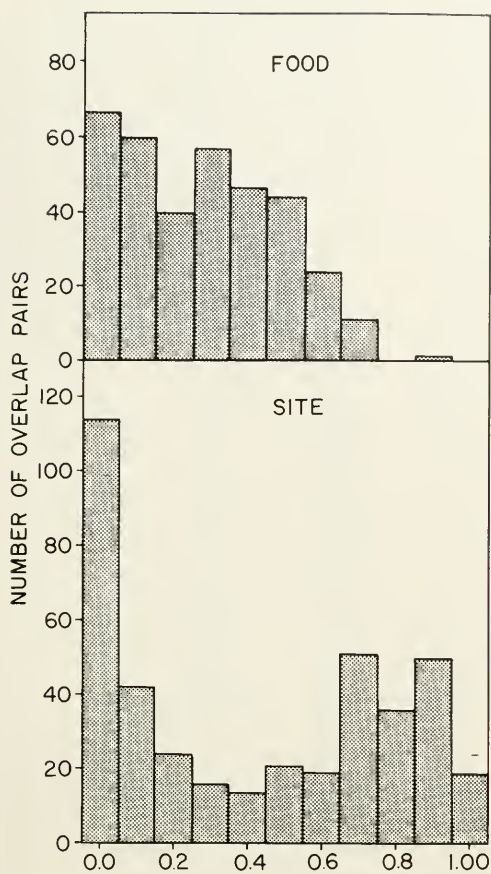


FIG. 192.—Number of overlap pairs among 29 species of lizards with respect to food and site.

mean number of overlaps in 4-space for forest species and non-forest species does not differ significantly (14.1 and 13.0, respectively, deleting species represented by only a single specimen). Also, the average amount of niche overlap in 4-space for forest and non-forest species (5.10 and 1.93, respectively) does not differ significantly.

SPECIES DIVERSITY

Quantitative comparison of communities involving the numbers of species (richness) and relative numbers of individuals of each species (equitability) has given rise to the concept of species diversity (see Margalef, 1958; MacArthur, 1965; and Pianka, 1966, for reviews).

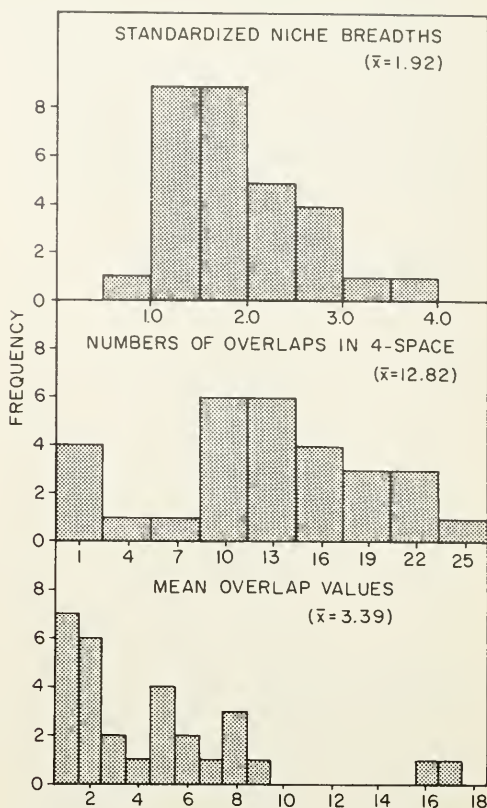


FIG. 193.—Standardized niche breadths, numbers of overlaps, and mean overlap values among 29 species of lizards.

MacArthur's (1957) "broken-stick model" was questioned by Hairston (1969), and Lloyd and Ghelardi (1964) proposed an equitability factor for the measure of fit of observed relative abundances to those predicted by MacArthur's model. Hurlbert (1971) criticized semantic, conceptual, and technical aspects of species diversity.

Despite Hurlbert's (1971) critique of diversity measurements, it is evident from the work of MacArthur (1965), Pianka (1967), Rosenweig (1975), and Cody (1975) that latitudinal gradients do exist in species richness and that there are differences in equitability in different communities. A quantitative expression of differences in diversity and equitability perhaps will be a useful method of

TABLE 31.—Niche Overlap Values (4-Dimensional) in Lizards and Amphisbaenians.
(° = 50% or more individuals in mature forest.)

SPECIES	No. of Overlaps	Mean Overlap	Total Overlap
<i>Gonatodes concinnatus</i> °	21	0.825	23.09
<i>Pseudogonatodes guianensis</i> °	12	6.320	176.90
<i>Thecadactylus rapicauda</i>	2	0.001	0.04
<i>Anolis chrysolepis</i> °	14	4.440	124.26
<i>Anolis fuscoauratus</i> °	18	5.200	145.51
<i>Anolis ortonii</i> °	15	3.280	91.85
<i>Anolis punctatus</i>	1	0.020	0.27
<i>Anolis trachyderma</i> °	11	4.960	138.87
<i>Anolis transversalis</i> °	11	0.200	5.72
<i>Enyalioides cofanorum</i> °	12	6.910	193.35
<i>Enyalioides laticeps</i> °	14	0.560	15.68
<i>Plica umbra</i> °	12	0.110	3.03
<i>Uracentron flaviceps</i> °	1	0.280	3.95
<i>Mabuia mabouya</i>	22	2.370	66.57
<i>Alopoglossus atriiventris</i> °	13	17.230	482.48
<i>Alopoglossus copii</i>	20	3.790	106.11
<i>Ameiva ameiva</i>	16	1.300	36.43
<i>Arthrosaura reticulata</i> °	11	6.750	188.94
<i>Bachia trinasale</i> °	11	0.600	16.67
<i>Dracaena guianensis</i>	10	2.490	69.73
<i>Iphisa elegans</i> °	11	3.500	98.10
<i>Kentropyx pelviceps</i>	17	4.190	117.78
<i>Leposoma parietale</i> °	24	7.000	196.00
<i>Neusticurus ecpleopus</i>	16	1.290	36.08
<i>Prionodactylus argulus</i> °	23	8.390	234.93
<i>Prionodactylus manicatus</i> °	19	15.500	217.00
<i>Ptychoglossus brevifrontalis</i>	5	0.030	0.77
<i>Tupinambis tequixín</i>	8	0.890	24.99
<i>Amphisbaena fuliginosa</i> °	2	0.002	0.06

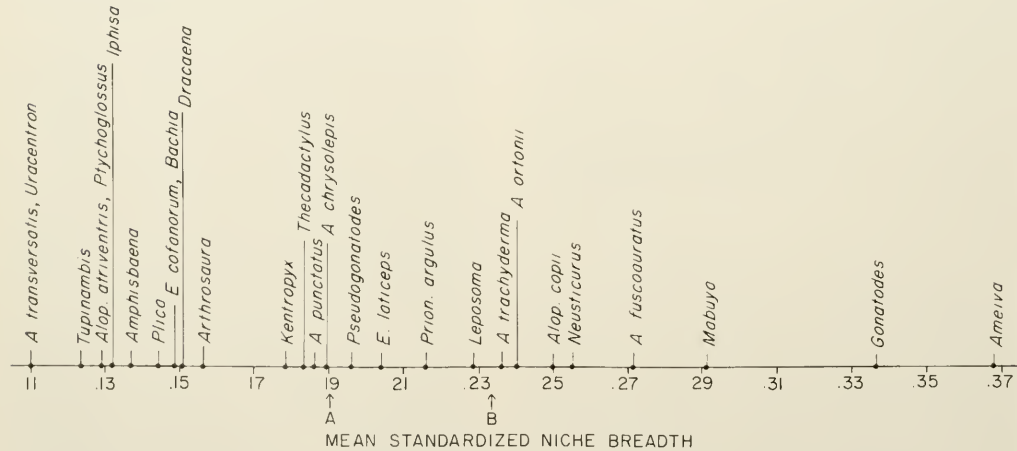


FIG. 194.—Relative positions of 29 species of lizards with respect to mean standardized niche breadths. A=mean for forest species; B=mean for non-forest species.

comparing communities, once sufficient numbers of communities have been studied. Crump (1971) used the Shannon (1948) index to provide measurements of diversity of 2.45 to 3.00 in amphibians and lizards in four major forest habitats in the vicinity of Belém, Brasil.

Indices of species diversity calculated by the Shannon (1948) function for three areas in the present study (Santa Cecilia, Lago Agrio, and Puerto Libre) are 4.30, 4.04, and 3.32, respectively. These values are positively correlated with the numbers of species at the three localities – 172, 93, and 72, respectively. Data on the numbers of individuals were based solely on specimens collected. These values are realistic for most species, of which all specimens observed were collected. However, for some of the more common species, such as *Anolis fuscoauratus*, *A. trachyderma*, *Eleutherodactylus croceinguinis*, *E. variabilis*, and some species of *Hyla*, no attempt was made to ascertain the actual abundance of individuals. Thus, equitability values are actually lower than those indicated.

Given our present state of knowledge, it is more informative to deal only in spe-

cies richness in comparing herpetofaunas in the American tropics (Table 32). In attempting to determine the number of species in a given area, it is nearly impossible to ascertain the complete fauna. Accumulation of additional species in the fauna is rapid in early sampling and then slows drastically (Fig. 195). In the Santa Cecilia area 75 percent of the species known in the fauna were collected in the first 100 man-days of field work; 1200 additional man-days were required to obtain the remaining 25 percent. When these data are analyzed in a more refined manner, a similar curve is obtained. In 1968 all field personnel recorded actual time spent in collecting, and a cumulative species list was maintained. After 40 hrs of collecting effort 43 species had been accumulated, in 80 hrs 56 species, 160 hrs 80 species, 320 hrs 101 species (Fig. 196).

Myers and Rand (1969) reported on the herpetofauna of Barro Colorado Island; they determined that on the basis of 47 years of collecting the herpetofauna consists of 100 species. This is by far the most completely sampled herpetofauna in the American tropics. Myers

TABLE 32.—Herpetofauna Species Richness at Four Localities in the American Tropics. (Number of species is followed by percentage of total in parentheses.)

	Santa Cecilia	Iquitos, Perú	Belem, Brasil ²	Barro Colorado Island, Panamá ³
Cacilians	5 (2.6)	3 (1.4)	3 (2.5)	1 (1.0)
Salamanders	2 (1.1)	1 (0.5)	1 (0.8)	2 (2.0)
Anurans	87 (47.2)	64 (30.6)	37 (31.5)	29 (29.0)
Turtles	6 (3.2)	9 (4.3)	3 (2.5)	5 (5.0)
Crocodylians	2 (1.1)	4 (1.9)	1 (0.8)	2 (2.0)
Lizards	29 (15.6)	38 (18.2)	24 (20.0)	21 (21.0)
Amphisbaenians	1 (0.5)	2 (1.0)	4 (2.5)	1 (1.0)
Snakes	53 (28.7)	88 (42.1)	47 (39.4)	39 (39.0)
TOTAL AMPHIBIANS	94 (51.1)	68 (32.5)	41 (34.2)	32 (32.0)
TOTAL REPTILES	91 (48.9)	141 (67.5)	79 (65.8)	68 (68.0)
TOTAL SPECIES	185	209	120	100

¹ Data from Dixon and Soini (1975, 1977) plus Dixon (pers. com.).

² Data from Crump (1971) and Duellman (unpublished).

³ Data from Myers and Rand (1969).

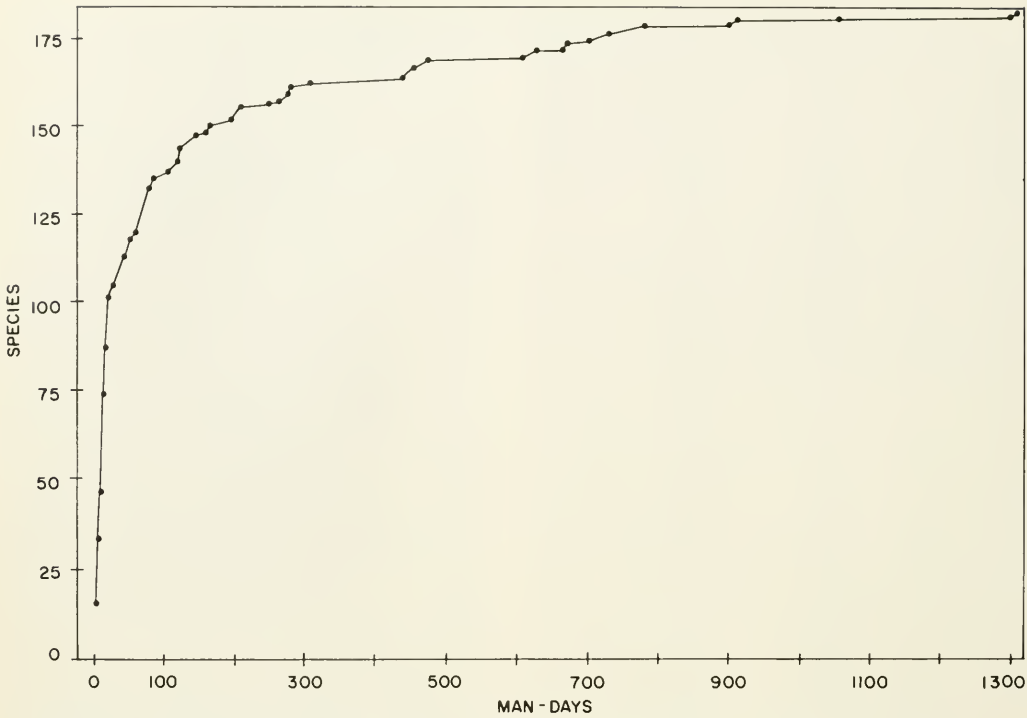


FIG. 195.—Effective sampling success of the herpetofauna in the Santa Cecilia area 1966-1973.

and Rand (1969) provided data on sampling success and noted that one collection made in the rainy season resulted in 43 percent of the herpetofauna in 91 man-hours of collecting and in the dry season 27 percent in 54 man-hours. In the first 54 man-hours of collecting in 1968 only 28 percent of the known number of species at Santa Cecilia was obtained; 35 percent was taken in the first 91 hours. On the basis of these data in comparison with the data from Barro Colorado Island, it can be assumed that few species have eluded the sampling at Santa Cecilia. I guess that no more than ten additional species (mostly snakes) might be found in the area. By projecting the curve in figure 195, it is postulated that approximately 1400 man-days would be required to add ten more species.

The data in table 32 reveal that, in comparison with the other sites, Santa Cecilia has a much higher percentage of anurans and much lower percentage of

snakes. Furthermore, at Santa Cecilia only 48.9 percent of the herpetofauna is composed of reptiles, whereas at the other localities 65-68 percent of the herpetofauna is made up of reptiles. If we calculate the percentage of reptiles that are snakes at the four localities, there is little difference — Santa Cecilia (58%), Iquitos (62%), Belém (59%), Barro Colorado Island (57%). Thus, the major discrepancy is the large number of species of anurans at Santa Cecilia. I believe that this is explainable by differences in climate equability at the different sites. Although the calculation of equability indices (Axelrod and Bailey, 1968) for Amazonian localities shows relative low equability throughout the Amazon Basin, their index is based solely on temperature. The richness of anuran species is dependent more on equable moisture. At Santa Cecilia there is no distinct dry season, whereas at Iquitos there are two dry seasons annually and at Belém and Barro Colorado Island pro-

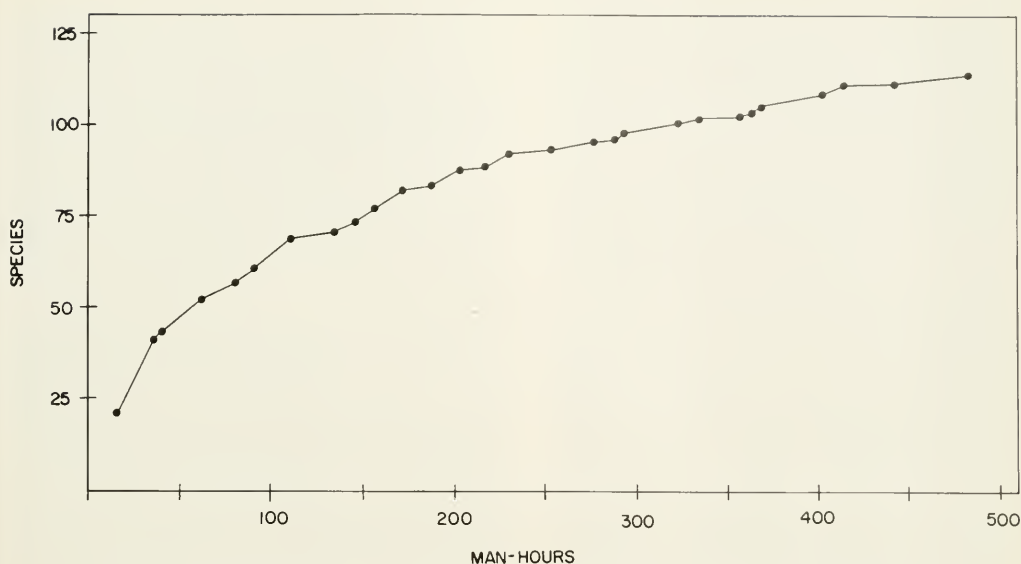


FIG. 196.—Sampling success of the herpetofauna at Santa Cecilia 7 June-27 July 1968.

longed dry seasons occur annually. On the Amazonian slopes of the Andes where moisture is abundant throughout the year, the vast majority of the herpetofauna at any given site consists of anurans; for example at the Río Azuela at 1700 m, 31 (88%) of the 35 species are anurans.

The question of relative abundances of species in tropical environments has been dealt with in birds by MacArthur (1969a), who concluded that as an area becomes uniformly packed with species their relative abundances become more uniform (see May, 1975, for digressions). Thus, if the Santa Cecilia area is viewed as a relatively stable environment, we might expect the species inhabiting primary forest, at least, to have relatively uniform abundances. Such is not the case. Even considering only those species that are at the same trophic level and in the same microhabitat, great discrepancies in relative abundance are found. For example, among frogs active on the forest floor by day the ratio of *Dendrobates parvulus* to *Edalorhina perezi* or *Lithodytes lineatus* must be in the order of 100:1; the ratio of *D. parvulus* to *Phylllobates femoralis* or *Colo-*

stethus marchesianus is about 2:1. Thus, of these brightly colored, diurnal terrestrial frogs, only one individual of *Edalorhina* or *Lithodytes* might be expected in a sample of 200 frogs. Explanations of these differences are more numerous than data to support them. Concepts concerning environmental patchiness, carrying capacity, fecundity, or competition can be invoked (also, inadequate sampling), but at present unchallengeable evidence is lacking.

Thus, in summary, the herpetofauna in the Santa Cecilia area is rich in species, especially anurans. Many species, especially smaller frogs and lizards, are extremely abundant, whereas others, especially snakes are seemingly rare. The disparity in abundances is due in part to different trophic levels, but this does not account for the differences in abundances within a given trophic level in a given microhabitat. The richness of the anuran fauna may be explained by the equability of moisture in comparison with other lowland forest areas.

DISCUSSION

Community ecologists and population biologists have provided us with a

variety of opinions and theories about tropical communities. With the exception of Patrick's (1966) work on freshwater communities, Janzen's (1973) analysis of insects, and Lowe-McConnell's (1975) studies on fishes, most studies on animal communities in the tropics have dealt with birds. Furthermore, nearly all ecological models pertaining to tropical communities have been directly or indirectly based on ideas derived from avian evidence. Birds differ from amphibians and reptiles not only in their obviously greater mobility and different physiologies and life histories, but also in attributes important in interactions within and between species in a community. These include structural specializations for restricted diets and diverse strategies for the pursuit or search for food, and complex intraspecific and interspecific social interactions including territoriality and ritualistic behavior, and migratory habits. Are herpetofaunal communities structured in the same way as bird communities? Are the models based on avian communities applicable to communities of frogs or lizards? Zaret (1976:673) raised the same points when he stated: "One wonders what would be the present state of theoretical ecology if scientists such as MacArthur, Cody, or May had considered fish populations instead of birds" In order to resolve these questions it is necessary to examine the major concepts of community dynamics and the corresponding data from the herpetological community under study.

Competition theory has played an important role in the development of concepts pertaining to the evolution, structure, and stability of communities (MacArthur, 1957; Hutchinson, 1958; Miller, 1969). Especially with respect to species richness in tropical communities, the idea of "species packing" (MacArthur, 1969b, 1970) has affected the design of competition and equilibrium models. Here we must consider: 1) the spectrum and abundance of available

resources; 2) the stability of the resources; 3) the extent of resource utilization by the members of the community; and 4) the amount of overlap in resource utilization by the members of the community. A tenet basic to the entire theory of competition is that one or more required resources must be limited (demand > supply) for effective competition to occur.

Most anurans and lizards in the community at Santa Cecilia are secondary consumers feeding mostly on a wide variety of insects. With the exception of the large mollusk-eating lizard, *Dracaena guianensis*, the only food specialists feed on ants or termites, both of which are extremely abundant. Niche-overlap values of 0.5 for prey are common among lizards and anurans (see Tables 22 and 24). Thus, due to the abundance of food throughout the year and the wide selection of prey taken by most anurans and lizards, it seems as though food is not a limited resource for these animals.

Anurans and lizards have minimal requirements for shelter in tropical rainforests. Diurnal species either retreat to subterranean cavities or perch on vegetation at night. Nocturnal species, all of which apparently are more susceptible to desiccation than most diurnal species, find abundant shelter amidst debris on the ground, beneath bark of trees, in crevices in logs and trees, on the undersides of leaves of trees, and in bromeliads. The super-abundance of such shelters and the wide dispersal of animals in the available shelters seem to preclude shelter as being a limited resource.

A third important resource is oviposition sites. For the lizards and those anurans that have terrestrial eggs, most of which are laid amidst debris on the ground, oviposition sites are nearly omnipresent. Although obviously more restricted, calling and oviposition sites for those anurans that deposit their eggs in water or in vegetation above water also are present in greater abundance than utilized by the community. Therefore,

oviposition sites do not seem to be a limited resource.

Most of the statements in the preceding three paragraphs probably also apply to the snakes, which are higher in the trophic structure, feeding primarily on small lizards and anurans. Occasionally food may be a limited resource for the few species that feed on small mammals or on other snakes.

What then are limited resources, if any, in this herpetological community? The primary forest can be viewed as an open system in that there are no (or only few) limitations of the resources needed for the populations of amphibians and reptiles living there. However, there may be distinct limitations of the resources available in the ponds and swamps where tadpoles develop (see p. 315). Nonetheless, the competition pressure, if indeed it does exist, does not explain the persistence of the richest anuran fauna known for any locality in the world.

It can be argued that the large numbers of species of amphibians and reptiles at Santa Cecilia can coexist due to the absence of, or very little pressure from, interspecific competition. The absence of interspecific competition is due to 1) the abundance of available resources, 2) structural heterogeneity of the environment, 3) climatic equability of the environment, and 4) differential utilization of resources spatially and temporally by the herpetofauna.

One might question the species packing of the herpetofauna. Are all of the available niches filled? Possibly not. Obvious absentees are herbivorous arboreal lizards, such as *Iguana*, and bromeliad-breeding and stream-breeding hyloid frogs. There are no nocturnal snakes feeding on centipedes, nor are there nocturnal snakes feeding on tadpoles in ponds. Certainly there must be many other less-obvious absentees.

It can be inferred from the discussion above that competition is not intense in the herpetofauna and therefore

populations are not at or near the carrying capacity of the environment. If competition does not play a significant role in the exclusion or diminution of numbers of individuals, what factors are operant on population control? Two factors, one abiotic and the other biotic, apparently are significant in regulating populations.

The primary abiotic factor is aperiodic environmental fluctuations, the most striking of which are periods of drought or periods of excessive rainfall. The former has an adverse effect on ephemeral aquatic breeding sites utilized by many anurans. Some small ponds and marshes frequently dry up resulting in the deaths of many tadpoles and eggs. Those species most severely effected by short droughts are the reproductive *r*-strategists (see discussion of fecundity in section on Reproductive Biology). Excessive rainfall results in flooding of areas that are usually dry. This results in some animals being driven from their normal shelters and the drowning of terrestrial eggs.

The primary biotic factor regulating population sizes in anurans and lizards is predation. In a lucid discussion of competition and predation in natural communities Connell (1975:475) stated: "Predation should be regarded as being of primary importance, either directly determining the species composition or in preventing competitive exclusion, except where the effect of predation is reduced for some reason." Furthermore, Connell (1975:484) concluded: "Since predation seems to be more intense in more benign physical conditions, competition should be prevented regularly in more benign regimes."

The evidence from the herpetofauna at Santa Cecilia strongly supports Connell's contentions. In tropical rainforest communities most anurans and lizards are abundant prey for diverse predators. Anuran eggs and tadpoles in ponds are preyed upon by birds, fish, and aquatic insects. Terrestrial anuran eggs and rep-

tile eggs are eaten by insects, snakes, and mammals; also the eggs are subject to attacks by mold. Snakes are important predators on frogs and lizards, these being preyed upon both night and day. Small mammals, especially opossums (*Marmosa*) and night monkeys (*Aotus*), seem to relish small frogs, mainly *Eleutherodactylus*, and sleeping *Anolis*. A variety of birds are known to prey on frogs and lizards.

Reproductive strategies of the component species are highly diverse (see section on Reproductive Biology). The population growth of the anurans and lizards is dependent primarily upon three density independent factors: 1) fecundity, 2) environmental fluctuations, and 3) predation. The latter is, or course, generally more significant in a prey species that has dense populations rather than one that is at a low density. Only if a species or group of species having considerable overlap in their utilization of available resources exceed the carrying capacity of these resources will competition become effective in limiting population growth or excluding species in the community. Theoretically, interspecific competition might occur most frequently among *r*-strategists, but one must remember that the *r*-strategists live in the least stable environments and also are subject to heavy predation pressure. Therefore, only after lengthy periods of favorable environmental conditions will their abundance negate the pressure from predation and will they reach the carrying capacity of the environment, which also will be reached more precipitously by a sudden lowering of the carrying capacity due to environmental fluctuations.

Thus, in answering the two original questions: Herpetological communities in aseasonal tropical forests are not structured in the same way as bird communities. The models generated on evidence from bird communities do not generally apply to herpetological communities.

Seasonal Versus Aseasonal Environments

Although it is common to compare tropical and temperate environments, for the reasons given on p. 289 I prefer to make the more meaningful comparison between the aseasonal tropical rainforest and seasonal environments, both tropical and temperate. Abiotically, the aseasonal tropical rainforest can be characterized by its equability in temperature, rainfall, and light. These equable conditions, plus the diversity of structural habitat and abundance of food provide a wide array of potential niches for a vast number of species, which are active throughout the year. By contrast, in seasonal environments, amphibians and many, if not all, reptiles are active only during part of the year. In temperate regions low temperatures necessitate hibernation during part of the year, whereas in the dry tropics aestivation is normal for amphibians and not uncommon for reptiles. In the seasonal environments there is less diversity of structural habitat and less diversity of and seasonality of food; thus, the number of potential niches is less numerous than in the tropical rainforest.

In his discussion of bird species richness in the tropics, MacArthur (1972: 216) stated: "... either the spectrum of resources, *K*, is greater in the tropics; the utilization per species, *U*, is less in the tropics; the overlap between species, *O/H*, is greater in the tropics; or the dimensionality of the environment, *C*, is greater in the tropics. Any of these can cause coexistence of the increased number of species that has been observed in the tropics. The embarrassment is that all are likely to be true, at least in some places!"

In comparison with herpetofaunal communities in seasonal environments, communities in aseasonal tropical forests certainly enjoy a greater spectrum of resources and greater dimensionality. I believe that these two factors alone can explain most of the differences that exist

in relative species richness. At least among the anurans and lizards, the vast majority of which are habitat generalists and feeding generalists, resource utilization does not seem to be any less in the tropics; in fact, in many cases utilization may be broader. If, as has been suggested previously, the abundance of prey for the secondary consumers in the rain-forest precludes competition for food, then niche overlap might be significantly higher in the tropics without being detrimental to any of the predators.

Unfortunately, few studies on herpeto-faunal communities have been undertaken. Pianka (1973, 1975, and references cited therein) compared lizard communities in desert regions in Africa, Australia, and South America. Fuentes (1976) compared Chilean and Californian lizard communities. Crump (1971) analyzed ecological distribution of lizards and amphibians at Belém, Brasil. Rand and Humphrey (1968) inferred interspecific competition in habitat selection among lizards at Belém, Brasil. Although the results of these studies, and others, show that species diversity and

richness vary between communities and that some ecological counterparts are absent in certain communities, they have not provided conclusive evidence for the substantiation of predicted differences between communities in aseasonal tropical environments and those in seasonal environments.

On the basis of the much larger numbers of species in aseasonal tropical communities than in seasonal communities, it is reasonable to postulate that potentially, interspecific competition would be greater in the aseasonal tropical communities. However, because of the structural heterogeneity in the aseasonal tropical environment and the abundance and diversity of food, in comparison with that in the seasonal environments, actual levels of competition are minimized far below the potential levels. Relative equability of temperature and moisture are the most important factors regulating the richness of herpetological communities. (Of course, the historical factor of the richness of the source material must be taken into consideration.)

BIOGEOGRAPHY

Now that the herpetological community at Santa Cecilia has been defined and the various aspects of the community interpreted, it is desirable to view the community in an historical context. In order to interpret certain historical aspects of the herpetofauna it is necessary to determine the distribution of the components of the fauna. Then we can attempt to answer the following questions: From where did the components of the herpetofauna come? How did they arrive at Santa Cecilia? How did the present community evolve?

DISTRIBUTION OF THE HERPETOFAUNA

The plotting of distributions of the 185 species in the herpetofauna at Santa

Cecilia resulted in the definition of eight general patterns of distribution (Fig. 197). The immediately obvious dichotomy is that four patterns involve the entire Amazon Basin (Fig. 197-A-D). Twenty-eight amphibians and 56 reptiles (=84 species or 45% of the fauna) are widespread in the basin. The other dichotomy involves species that are essentially restricted to the upper part of the basin (Fig. 197E-H): 66 amphibians and 35 reptiles (=101 species or 55% of the fauna) are so restricted.

The most widespread pattern (Fig. 197A) includes the humid lowland tropics of the Amazon Basin, the Guianas, lower Central America, and the forested Pacific lowlands of Colombia and Ecuador. Some species having this pattern also occur on the Caribbean lowlands of

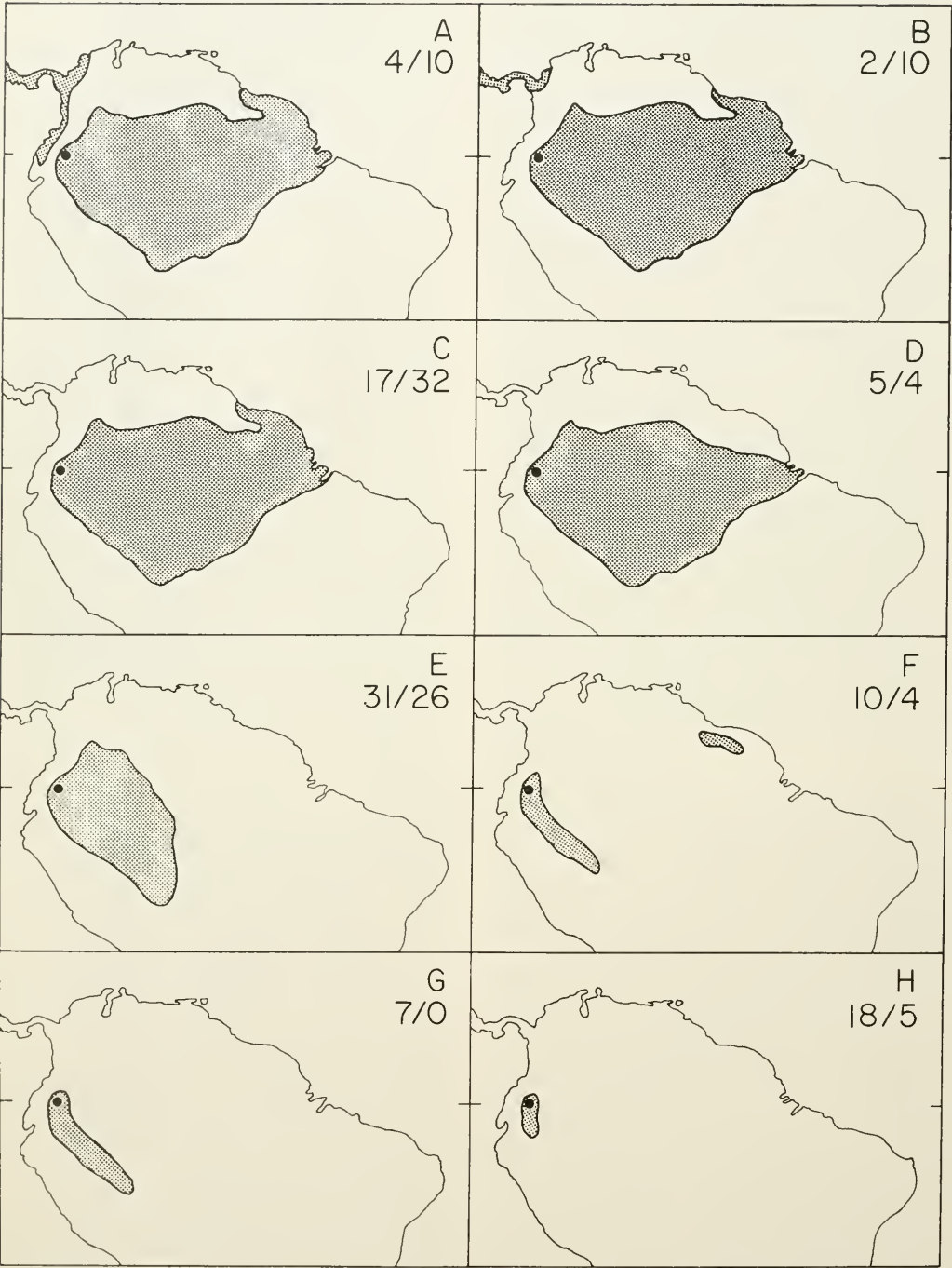


FIG. 197.—Distribution patterns of species in the herpetofauna at Santa Cecilia. Numbers are amphibians/reptiles; the dot is Santa Cecilia.

Colombia and Venezuela and/or the lowlands of southeastern Brasil. Examples of these wide-ranging species are *Bufo marinus*, *Thecadactylus rapicauda*, and *Boa constrictor*. Most of the species in this group seem to have wide habitat tolerances and are not confined to wet forests.

The second pattern (Fig. 197B) is like the former except for the exclusion of the Pacific lowlands of Colombia and Ecuador. Examples include *Phrynohyas venulosa*, *Kinosternon scorpioides*, *Ameiva ameiva*, and *Leptodeira annulata*.

The most common pattern among species that range through the entire Amazon Basin also includes the Guianas but does not include northwestern South America or lower Central America (Fig. 197C). Examples of this wide-spread component include *Pipa pipa*, *Hyla geographica*, *Anolis chrysolepis*, *Dracaena guianensis*, and *Micrurus lemniscatus*. A much smaller number of species occur throughout the basin but do not extend into the Guianas (Fig. 197D). Examples of these include *Leptodactylus rhodomystax*, *Drymoluber dichrous*, and *Micrurus spixii*.

Among those distributional patterns that include only the upper part of the Amazon Basin, the largest group of species (57=31%) inhabit most of the upper part of the basin (Fig. 197E). Examples of this pattern include *Dendrophryniscus minutus*, *Phyllomedusa tarsius*, *Paleosuchus trigonatus*, *Anolis trachyderma*, *Atractus elaps*, and *Bothrops castelnaudi*. A small group of amphibians, including *Oscacilia bassleri*, *Bolitoglossa peruviana*, *Eleutherodactylus ockendeni*, *Hyla bifurca*, *Hyla rhodopepla*, *Chiasmocleis bassleri*, and *Hamptophryne boliviana*, occurs only along the western edge of the basin from Colombia to southern Perú or Bolivia (Fig. 197G). Seventeen species have a similar pattern except that they also occur in the Guianas (Fig. 197F). Examples of this group are *Lithodytes lineatus*, *Hyla fasciata*, *Phryno-*

hyas coriacea, *Dipsas indica* and *Ninia hudsoni*.

The most restricted pattern is that encompassing only the upper edge of the basin in Ecuador and adjacent Colombia (Fig. 197H). The 18 amphibians and five reptiles in this group are: *Microcaecilia albiceps*, *Bolitoglossa ecuadorensis*, *Eleutherodactylus diadematus*, *E. martiae*, *E. nigrovittatus*, *E. orphnolaimus*, *E. paululus*, *E. pseudoacuminatus*, *E. quaquaversus*, *Bufo glaberrimus*, *Colostethus sauli*, *Hemiphractus proboscideus*, *Hyla bokermanni*, *Nyctimantis rugiceps*, *Centrolenella midas*, *C. resplendens*, *Chiasmocleis anates*, *Syncope antenori*, *Alopoglossus copii*, *Atractus occipitoalbus*, *Helicops petersi*, *Leimadophis sp.*, and *Oxyrhopus formosus*.

The proximity of Santa Cecilia to the base of the Andes (± 40 km) necessitates an examination of the altitudinal distribution of the species in the Santa Cecilia herpetofauna on the eastern face of the Andes in Ecuador. Many of the species (37%) occurring at Santa Cecilia do not ascend the slopes at all; their distributions terminate by 400 m elevation (Fig. 198). At elevations above 600 m, 56 percent of the species are no longer present, and only 28 percent extend above 1000 m. Six frogs (*Eleutherodactylus acuminatus*, *E. conspicillatus*, *E. quaquaversus*, *Osteocephalus buckleyi*, *O. taurinus*, and *Bufo typhonius*) and one reptile (*Leimadophis reginae*) occur above 1500 m. A zone of luxuriant cloud forest occurs at elevations between 1100 and 1800 m on the eastern face of the Andes in Ecuador. This cool, moist forest apparently presents environmental conditions beyond the tolerances of most lowland reptiles and many amphibians. Pond-breeding frogs are limited further by the near absence of ponds on the Andean slopes.

Although the distributions of species of amphibians and reptiles in the Amazon Basin are not known in great detail, sufficiently thorough sampling has been

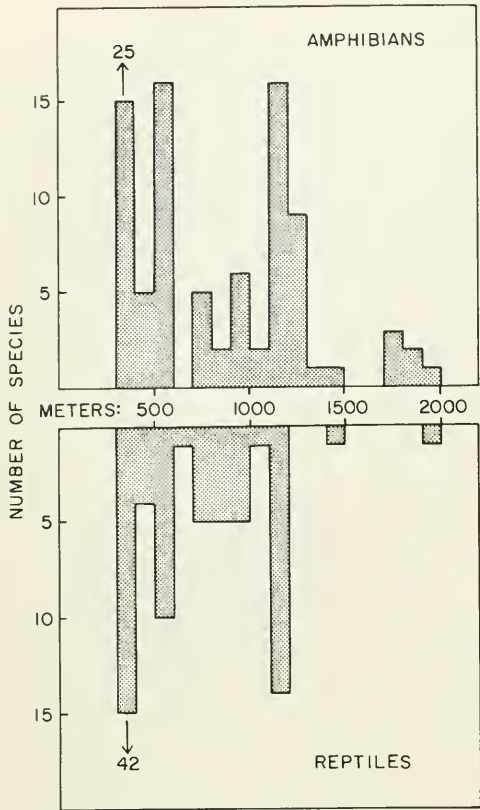


FIG. 198.—Upper elevational limits on the eastern slopes of the Andes of species in the herpetofauna at Santa Cecilia.

done at Iquitos, Perú (Dixon and Soini, 1975, 1976) and Belém, Brasil (Crump, 1971) to allow meaningful comparisons of these with Santa Cecilia and with the well-known fauna on Barro Colorado Island, Panamá (Myers and Rand, 1969). Faunal comparisons were made by the method developed by Duellman (1965, 1966) of determining a faunal resemblance factor by means of the formula $FRF = 2C / (N_1 + N_2)$, where N_1 and N_2 are the numbers of species in any two given faunas, and C is the number of species common to both faunas. As would be expected the greatest amount of faunal resemblance is between Santa Cecilia and Iquitos and the least between Santa Cecilia and Barro Colorado Island (Table 33).

There are numerous species of rep-

TABLE 33.—Comparison of Herpetofaunas at Four Tropical Localities.
(**Boldface** numbers are actual numbers of species at a locality; **Roman** numbers are the number of species in common between localities; *italicized* numbers are the faunal resemblance factors (see text for explanation). In each group, the first row is amphibians, second row is reptiles, and third row is the total of amphibians and reptiles.)

	Santa Cecilia	Iquitos, Perú	Belém, Brasil	Barro Colorado Island, Panamá
Santa Cecilia, Ecuador	94	53	22	4
	91	83	42	13
	185	136	64	17
Iquitos, Perú	.654	68	23	3
	.715	141	60	19
	.690	209	83	22
Belém, Brasil	.379	426	40	2
	.494	.545	79	15
	.421	.506	119	17
Barro Colorado Island, Panamá	.032	.030	.028	32
	.163	.182	.204	68
	.119	.142	.155	100

tiles that are widespread in the Amazon Basin that do not occur at Santa Cecilia. Many of these are aquatic species (*Helicops leopardinus*, *H. polylepis*, *Hydrops martii*, *H. triangularis*, *Pseudoeryx plicatilis*, *Phrynos nasutus*, *Podocnemis expansa*, *P. sextuberculata*, *P. unifilis*, *Melanosuchus niger*, and *Paleosuchus palpebrosus*) that characteristically inhabit quiet rivers or swamps associated with flood plains. The gradients of the streams at Santa Cecilia and the near absence of swamps associated with rivers apparently preclude the existence of these aquatic species at Santa Cecilia. Some other species (*Iguana iguana*, *Plica plica*, *Kentropyx calcaratus*, *Amphisbaena alba*, *Oxybelis aeneus*, and *O. fulgidus*) are usually associated with more open forest than that occurring naturally at Santa Cecilia. Certain species at Santa Cecilia

(e.g. *Ameiva ameiva*, *Mabuya mabouya*, *Hyla rubra* and *Bufo marinus*) also belong in this category. These are "weed" species that disperse rapidly along roads and other man-made clearings. Perhaps the four species mentioned for Santa Cecilia are more vagile than the others, which in time might be expected to reach Santa Cecilia.

ORIGIN OF THE HERPETOFAUNA

The many recent studies on plate tectonics provide an overwhelming amount of evidence that South America was an isolated land mass throughout most of the Tertiary. The breakup of Western Gondwanaland commenced in the early Cretaceous (± 125 million years BP) (Larson and Ladd, 1973), and the separation of Africa from South America occurred in the late Cretaceous (± 90 million years BP) (Grant, 1971). Raven and Axelrod (1972) summarized evidence for direct biotic migration between South America and Australia via Antarctica in the Eocene and probably well into the Oligocene (± 38 million years BP). After the initial breakup of Pangaea in the Triassic there was no direct land connection between North America and South America until the late Tertiary; their positions converged beginning in the mid-Cretaceous (Dietz and Holden, 1970). Holden and Dietz (1972) and Mafait and Dinkelman (1972) provided evidence for an island arc between nuclear Central America and South America in the Cretaceous and early Tertiary; this arc moved northeastward (in relation to South America) through most of the Tertiary and formed the present Lesser Antilles. The region of lower Central America formed as a volcanic archipelago in the Oligocene with additional land emerging and coalescing with nuclear Central America about 10-12 million years BP and finally with South America about 5.7 million years BP (Dengo, 1969; Emiliani, Gaertner, and Lidz, 1972; Haffer, 1970; Whitmore

and Stewart, 1965). Further biological evidence for faunal interchange between Central America and South America was presented by Rosen (1975), Savage (1974), and Tedford (1974).

Raven and Axelrod (1974:549) summarized the isolation of South America: "Judging from the geology of the region, and the relative motions of the plates South America was more accessible to immigration from Africa than from North America until after the Early Eocene. Subsequently, more and more insular connections with North America were established, culminating with a direct land connection only 5.7 my BP. Clearly, the history of South American biota has been one of evolution in isolation of an initial West Gondwanaland stock shared with Africa. To South America have come many cool temperate Australasian plants and animals, essentially overland until the Eo-Oligocene, and by overseas long-distance dispersal subsequently. South America contributed increasingly to the flora of tropical and subtropical North America during the Tertiary, it received immigrants from temperate North America only as the Cordillera rose in the late Neogene, at which time it also contributed montane tropical taxa to Central America."

Summaries of the paleogeography of South American amphibians and reptiles were presented by Reig (1968) and Cracraft (1974). The history of specific groups has been treated by various authors - caecilians (Estes and Wake, 1972), salamanders (Wake, 1966), anurans (Cei, 1968; Estes, 1975; Estes and Reig, 1973; Savage, 1973), crocodilians (Sill, 1968), turtles (Simpson, 1950), lizards (Estes and Price, 1973); Vanzolini, 1968). Laurent (1973) briefly compared the herpetofauna of Africa and South America.

Of the 25 family groups of amphibians and reptiles comprising the fauna at Santa Cecilia, 17 are of Gondwanian origin and eight are Laurasian in origin (Table 34). The primary sources of the

TABLE 34.—Paleogeography of family groups in Santa Cecilia Herpetofauna.

FAMILY GROUP	CENTER OF ORIGIN	SOURCE OF S. AMER. GROUP	APPEARANCE IN S. AMER.
Caeciliidae	Gondwanaland	S. Amer.	Paleocene
Plethodontidae	N. Amer.	C. Amer.	Post-Miocene
Pipidae	Afr.-S. Amer.	S. Amer.	Paleocene
Leptodaetylidae	S. Amer.	S. Amer.	Eocene
Bufonidae	Afr.-S. Amer.	S. Amer.	Paleocene
Dendrobatidae	S. Amer.	S. Amer.	?
Hylidae	S. Amer.	S. Amer.	? Eocene
Centrolenidae	S. Amer.	S. Amer.	?
Microhylidae	Gondwanaland	S. Amer.	?
Ranidae	Africa	N. Amer.	Post-Miocene
Cheliidae	Aust.-S. Amer.	S. Amer.	Cretaceous
Kinosternidae	N. Amer.	N. Amer.	Post-Miocene
Testudinidae	Laurasia	N. Amer.	? Miocene
Crocodylidae	Afr.-S. Amer.	S. Amer.	Triassic
Gekkonidae	Gondwanaland	S. Amer.	Paleocene
Iguanidae	S. Amer.	S. Amer.	Cretaceous
Scincidae	Laurasia	N. Amer.	Post-Miocene
Teiidae	S. Amer.	S. Amer.	Cretaceous
Amphisbaenidae	Laurasia	N. Amer.	? Miocene
Aniliidae	? Laurasia	N. Amer.	?
Boidae	Gondwanaland	S. Amer.	Cretaceous
Colubrinae	Laurasia	N. Amer.	Post-Miocene
Xenodontinae	S. Amer.	S. Amer.	Cretaceous
Elapidae	Gondwanaland	S. Amer.	Cretaceous
Crotalidae	Laurasia	N. Amer.	?

familial components are South America (16), Central America (1); and North America (8). Thus, the members of most of the familial groups evolved in South America. Some groups, such as the Testudinidae, Amphisbaenidae, Aniliidae, and Crotalidae apparently entered South America from North America prior to the closure of the Panamanian Portal in the early Pliocene. Other North and Central American groups probably did not enter South America until the Pliocene; these include bolitoglossine plethodontids, *Rana*, *Kinosternon*, scincids, and colubrine colubrids. The xenodontine colubrids underwent their adaptive radiation in South America, but some stocks evidently migrated northward into nuclear Central America prior to continuous land connections in the early Pliocene. As xenodontine isolates, genera such as *Leptodeira* (Duellman, 1958) and *Rhadinaea* (Myers, 1974) evolved and speciated in México and Central America. Later, probably in the Plio-

cene, some species in these genera dispersed into South America.

It is safe to assume that by the end of the Pliocene (± 1.8 million years BP) all of the component families and most, if not all, of the genera of amphibians and reptiles existed in South America in or peripheral to the Amazon Basin.

TERTIARY AND QUATERNARY HISTORY OF THE AMAZON BIOTA

The interpretation of the historical biogeography of tropical regions has been obfuscated by the dogmatic beliefs that the tropical rainforests of the world are ancient environments that have changed very little in millions of years, and that they were unaffected by climatic fluctuations in the Pleistocene (see Schwabe, 1969, as a recent example). Moreau (1963, 1969) summarized evidence for climatic changes in the Pleistocene in tropical Africa and used this

evidence for explaining certain patterns of distribution of the biota. Haffer (1969), Vanzolini and Williams (1970), and Vuilleumier (1971) introduced the same concepts in South American biogeographic analyses. The geological palynological, and climatic evidence for fluctuating environments in the equatorial tropics in South America were documented thoroughly by Müller (1973) and Haffer (1974), and the palynological evidence was further summarized by Van der Hammen (1975).

Haffer (1969, 1974, 1975) provided evidence from avian distributions and patterns of differentiation for six persistent forest refugia in the Amazon Basin. Vanzolini and Williams (1970) proposed four core areas for the differentiation of *Anolis chrysolepis*; they proposed an evolutionary model of three expansions and two contractions of forest environments. Müller (1973) recognized four major dispersal centers in the Amazon Basin; the basis for his centers are coincidental distributional limits of vertebrates. On the basis of plant distributions, Prance (1973) provided evidence for forest refugia that are remarkably consistent with those proposed by Haffer but more extensive than Vanzolini and Williams' core areas. Studies on heliconian butterflies by Brown (1972) and Brown and Mielki (1972), on hylid frogs by Duellman (1972b) and Duellman and Crump (1974), and on leptodactylid frogs by Heyer (1973) provide additional support for the hypothesis of distributional discontinuities and patterns of differentiation being correlated with the existence of forest refugia during arid climatic phases in the Quaternary.

Although the details of the Tertiary geologic history of the Amazon Basin are not known, Haffer (1974:128) stated: "Probably the sediments were deposited in large swamps and marshes, and on vast flood plains crossed by numerous meandering streams flowing into a huge inland sea, which connected to

the sub-Andean basin to the west and with the Atlantic Ocean to the east. . . . During the Late Pliocene (end of Tertiary time) the Amazon valley probably was covered by a large lake with a narrow eastern outlet. . . . The final uplift of the Andes and of the upper Amazonian lowlands (previously covered by a huge inland sea) led to the establishment of the eastwardly directed drainage pattern in Amazonia during early Quaternary time. The rivers shaped their present beds cutting into the Tertiary formations during the Pleistocene periods of lowered world sea level and depositing sediments in the broad Amazon valley during periods of raised sea level (interglacials), when a large portion of the Amazon valley was flooded."

The uplift of the central and northern Andes began in the Miocene, but geological (Petersen, 1958) and palynological (Van der Hammen, 1966; Van der Hammen and Gonzalez, 1964) evidence indicates that the Andes underwent their greatest uplift at the end of the Pliocene and at the beginning of the Pleistocene (± 1.8 million years BP).

Haffer (1974:135) summarized the existing evidence on Pleistocene climates in the American tropics and concluded: "Two major events determined environmental conditions in tropical South America during this time interval. First, the main uplift of the Andes during the Late Pliocene and Early Pleistocene led to the vast expansion of dense forest onto the fully emerging upper Amazon basin. This forest also reached far to the north to the slopes and lowlands around the mountains along the Colombian Andes and south on the eastern slope to Bolivia. Second, the alterations of humid and dry climatic periods in the tropics, caused by the Pleistocene periodicity of world climate, resulted in periodic shrinkage and expansion of the lowland forests and non-forest vegetation, respectively. At the same time, changing world sea levels led to the exposure of the continental shelves in glacial times, which increased the

width of the coastal lowlands, and to the flooding of part of the present coastal plains and of the Amazon Valley during interglacial periods."

Post-Pleistocene changes in the Amazon Basin have consisted on alternating humid and arid climatic phases. Geomorphological, palynological, and paleobotanical evidence places two arid phases at about 11,000 and 2500-4000 years ago (Dammuth and Fairbridge, 1970; Haffer, 1974; Vanzolini and Ab'Saber, 1968). During these arid phases the vast Amazonian rainforest became fragmented, and the nonforest environments (savanna and cerrados) expanded. At the time of the last arid phase (2500-4000 years BP) the Amazon forest was probably completely separated into lower and upper Amazonian forest by a continuous dry belt extending from southern Venezuela to northeastern Brazil; this area today receives less than 2500 mm of rainfall annually. During the most severe arid phases tropical rainforest persisted in certain areas due to favorable local edaphic, topographic, and climatic conditions (Haffer, 1969, 1974).

These post-Pleistocene climatic changes and concomitant restriction and expansion of the Amazonian rainforest are the environmental bases for patterns of distribution and speciation seen in northern South America today (Haffer, 1969, 1974; Müller, 1973; Vanzolini, 1973; Vanzolini and Williams, 1970).

The upper part of the Amazon Basin apparently emerged from the mid-continental lake and became covered with rainforest at about the beginning of the Pleistocene (± 1.8 million years BP). This is approximately 3.9 million years after the establishment of the continuous land connection between Central America and South America. During this time the northern Andes were low rolling hills covered with tropical or subtropical forest (Haffer, 1975); thus, dispersal routes were available for Central American groups to enter the Amazon Basin.

EVOLUTION OF THE HERPETOFAUNAL COMMUNITY

Santa Cecilia is located in one of the largest of the hypothesized forest refugia, the Napo Refugium; the Ucayali Refugium lies to the south in Perú (Haffer, 1969). Coalescence of the forests in these refugia must have been more nearly continuous throughout the Quaternary than the meeting of either of these forests with others eastward in the Amazon Basin. Lying close to the base of the Andes, Santa Cecilia also must have received fauna from the Andean slopes when climates were depressed at times of Andean glaciation. Thus, throughout the Quaternary the Santa Cecilia area was a humid tropical forest and at various times was in contact with other forested areas to the south and east and at other times was isolated from these forests. Furthermore, the Santa Cecilia area was in continuous contact with the forested Andean slopes and in more or less continuous contact with peripheral Amazon Basin forests extending south into Perú and perhaps Bolivia and north into Colombia and at times eastward from there to the Guiana Shield. These various periods of contact and isolation resulted in restricted distribution patterns (Fig. 197-E-II).

The fluctuating environmental conditions in the Amazon Basin provided a scenario for the processes of speciation. Populations of species were isolated in ecological islands and differentiated; coalescence of formerly isolated environments resulted in the reunification of populations in these environments. If the isolated populations had not differentiated to the point of reproductive isolation, introgression would occur when and where the populations were reunited. If the isolated populations had differentiated to the point of genetic incompatibility, their reunification could have any one of three results: 1) Two populations not dependant on a limited resource can coexist in geographic sym-

patry. 2) Two populations equally adapted for utilization of a limited resource will exist in geographic parapatry. 3) If one of two populations was more effective in utilizing a limited resource than the other, the former population will expand through the range of the latter population. Thus, the latter is an example of competitive dominance that theoretically will result in the extinction of one population. The second situation is an example of competitive exclusion and may explain the restricted ranges of many species in the Amazon Basin. The first alternative provides us with an explanation of species richness in one community.

Because of aseasonal reproductive cycles, complete absence of pair bonds, and frequent mating and reproduction, most populations of tropical amphibians and reptiles probably are highly heterogeneous genetically and therefore are likely to develop genetic differences during very brief periods in isolation. Introgression of genetically compatible isolates may explain some of the bewildering mosaics of variation seen in some species, whereas differentiation to the point of reproductive isolation allows the coexistence of several closely related species.

The latter example was used by Duellman and Crump (1974) to explain the coexistence of three species in the *Hyla parviceps* group at Santa Cecilia, and the same explanation can be applied to the *Hyla leucophyllata* group, five species of which coexist at Santa Cecilia. The species differ in mating calls, oviposition sites, and kinds of ponds used for reproduction. The same explanation can be applied to the three species of *Chiasmocleis*, the *Leptodactylus pentadactylus* group, the *Hyla geographica* group, *Osteocephalus*, the two species of *Enyaliodes*, the two species of *Alopoglossus*, and perhaps several others.

The herpetofauna at Santa Cecilia is composed mainly of forest-adapted species that either are restricted to the upper Amazon Basin or widespread in the Amazon Basin. Probably the majority of the former group and some of the latter group evolved in the Napo and Ucayali refugia. Other components of the fauna are inhabitants of the Andean slopes that barely invade the Amazon Basin, whereas a few non-forest species (*Bufo marinus*, *Hyla rubra*, *Ameiva ameiva*, and *Mabuya mabouya*) are recent immigrants along the river playas.

EPILOGUE

During the ten years that I have been studying Amazonian herpetofaunas, I have come to realize several shortcomings of the study of the community at Santa Cecilia. How many times must investigators wish upon the completion of a study that they could begin again and do it right? On the basis of experience at Santa Cecilia, I offer the following suggestions for the study of herpetological communities in tropical rainforests:

1. Data needed for thorough community analyses are derived in part from observations of the animals and in part from examination of preserved specimens. These two kinds of data cannot

be collected at the same time and place without the collection of specimens interfering with the natural populations. Because both kinds of data are needed from throughout the year, a large study area could be divided into two parts – one for observations and one for collecting. A long term study in a smaller area could be divided temporally with intensive collecting following a period of observation.

2. In order to obtain meaningful data on reproductive cycles it is necessary to have large series of specimens from throughout the year. It is doubtful if adequate samples of some lizards and most snakes could be obtained in fewer

than five years. Data on reproductive cycles of individuals need to be obtained by mark and recapture studies. In species-rich tropical communities it is unfeasible to attempt mark and recapture studies on all species. Instead selected species differing in reproductive modes and habits should be investigated.

3. Analyses of food should be based not only on taxonomic content but also on volume; analyses also should take into account size of predator and prey and time of year. Thus, series of specimens of all size classes are needed from throughout the year.

4. Concomitant with mark and recapture studies designed to obtain data on reproductive cycles it is possible to obtain data on growth, longevity, and population turnover. Such data are practically non-existent for tropical species.

5. The most accurate way I know of obtaining data on the numbers of individuals and species is to clear the forest. A study area one kilometer square should be bordered by a 50 m wide cleared area. Systematic paring of the edge of the study by bulldozers and felling trees into the cleared area provides a method of sampling the fauna from the shallow subterranean level to the canopy. A thorough sampling of a systematically cleared forest will provide a much more accurate assessment of actual numbers of individuals of species than now available.

Care must be exercised in applying ecological and population models. At the present time our understanding of a minimal data base on tropical communities is so limited that only the most general conclusions can be inferred. Models based on data from one group of organisms or from one environmental regime do not necessarily apply to other groups of organisms or to other environmental regimes. Before we have an adequate understanding of tropical communities much greater amounts of research funds must be designated for field studies.

There is a great sense of urgency in the collection and study of the Amazonian biota. Within the past few years man in his frenetic pace of exploitation has devastated millions of hectares of the Amazonian forest, once the most vast area of tropical wilderness on earth. Data on the taxonomy and distribution of species can be accumulated by extensive collecting throughout the basin. However, the data so accumulated in such salvage operations will provide only limited biological information on the fauna. The studies of communities necessary to acquire an understanding of tropical faunas and their ecology require the preservation of natural regions. Intelligently selected areas of sufficient size (see Terborgh, 1975) will result in the conservation of biotic communities and provide areas for the study of communities. The Republic of Ecuador, which has set a conservation precedent in the Galapagos Islands, currently is evaluating the Proyecto Cayambe-Coca proposed by the FAO of the United Nations. The Proyecto Cayambe-Coca calls for the establishment of a national park and biological preserve extending from Volcán Cayambe in the Andes to the Río Coca in the Amazon Basin. This area includes parts of the cloud forest on the eastern face of the Andes and rainforest in the upper reaches of the Amazon Basin. If this projected preserve becomes a reality, a significant part of the fauna associated with the Napo Refugium will be conserved for future study.

The community at Santa Cecilia reported upon here is gone. The expanse of primary forest along the banks of the Río Aguarico has been replaced by *milpas*, *yuca*, and *plátanos*, most of which are abandoned in a few years to be taken over by dense bushes and vines or badly eroded. Man through his various cultural levels of utilization, exploitation and eventual destruction has destroyed this biological community in a few short

years. We can only hope that enlightened government agencies will set aside substantial natural preserves in an effort

to prevent the "Green Hell" from becoming the "Red Desert" (Goodland and Irwin, 1975).

RESUMEN

Este estudio está basado en observaciones y especímenes obtenidos durante 48 hombres-meses de trabajo de campo en la alta cuenca del Amazonas en Ecuador. El sitio principal de estudio fue un área de cerca de 3 kilómetros cuadrados en Santa Cecilia, en el Río Aguarico, a 340 m de altitud, con 00°03' N, 76°59' W como coordenadas. Cuatro otras localidades del Río Aguarico (Dureno, Lago Agrio, Puerto Libre, y Puerto Ore) fueron estudiadas con menor intensidad. El material reunido en las cinco localidades consiste de 9035 especímenes de 185 especies, mientras que de sólo Santa Cecilia 7765 especímenes de 173 especies fueron colectados. Taxonómicamente, esta fauna está compuesta por 5 especies de *Gymnophiona* (3 presentes en Santa Cecilia), 2 de *Caudata* (2), 87 de *Anura* (81), 6 de *Testudines* (6), 2 de *Crocodylia* (2), 29 de *Sauria* (27), 1 de *Amphisbaenia* (1), y 53 de *Serpentes* (51).

La región alrededor de Santa Cecilia tiene un bajo relieve (< 20 m) con varios arroyuelos y depresiones. El Río Aguarico es un río de aguas blancas, y el Río Conejo un arroyo sinuoso de aguas lentas. Existen allí dos lagos permanentes y hay numerosos pantanos en las depresiones. El clima es típico Af (del sistema de Köppen) con fluctuaciones aperiódicas pero sin estaciones anuales distintas. Las fluctuaciones diarias de la temperatura son de cerca de 10° C, y la diferencia en promedios mensuales de cerca de 2° C. Las temperaturas máxima y mínima registradas han sido 37° y 17° C. La precipitación anual para el período Julio 1971-Junio 1972 fue de 4289 mm, siendo Marzo el mes más lluvioso (con 619 mm) y Agosto el más seco (con 220 mm). El más extenso período sin lluvia duró cinco días, mien-

tras que la más abundante lluvia en 24 horas fue de contuvo 390 mm.

La vegetación natural de Santa Cecilia es selva húmeda tropical de tipo primaria, la cual está mejor desarrollada en suelos planos bien drenados. Los más altos árboles forman una techumbre a 30-35 m de altura. Un segundo estrato se forma a 15-20 m de altura, y un tercer estrato a 8-12 m. El suelo está cubierto de hierbas y helechos (10-25 cm de altura), donde una capa continua de hojarasca está presente.

Selvas secundarias, resultantes de intervenciones humanas o de caídas naturales de árboles, están caracterizadas por una sucesión forestal sin estratificación, dominada frecuentemente por *Cecropia* de alturas de 10 a 12 metros. En estas selvas hay densos matorrales y poca hojarasca; grupos de bambúes de 15 a 18 m de altura se encuentran repartidos a lo largo de este tipo de selva.

Depresiones del terreno en ambas clases de selvas contienen agua al menos intermitentemente. Estos pantanos difieren de las pequeñas y poco profundas depresiones que fuertes lluvias se convierten en grandes pantanos semipermanentes sólo después de la fuertes lluvias. Los pantanos en la selva primaria suelen tener varias palmeras espinosas; aquellos en selvas secundarias suelen estar densamente poblados con *Heliconia*. Ciénegas en claros hechos por el hombre tienen pastos, varias aráceas, y pequeñas *Heliconia*.

Para los propósitos de análisis ecológicos, las siguientes categorías terrestres fueron reconocidas: selva primaria, selva secundaria, borde de selva, bambú, claro, y terrenos cultivados. Los ambientes acuáticos fueron designados como pantano, ciénega, lago, río, y arroyo.

Uno de los más difíciles problemas

encontrados en este estudio de la herpetofauna fue la identificación de las especies. Como una ayuda a futuros trabajos, claves ilustradas de la herpetofauna son provistas.

En el recuento de las especies, al número de especímenes de cada localidad, lo sigue una descripción diagnóstica de la especie en cuestión. En las secciones sobre presencia e historia natural, se incluyen datos sobre el habitat, actividad, reproducción, y alimento. En los recuentos pertinentes hay discusiones sobre los renacuajos, cantos nupciales, variación, status taxonómico, y nomenclatura.

Un análisis de los modos reproductivos anuales revela que los anuros son capaces de reproducirse a lo largo del año. La lluvia parece ser el más importante factor con influencia sobre el período de reproducción; la mayoría de las especies responden con un incremento de la actividad reproductiva a los incrementos de lluvia. Algunas especies se reproducen sólo luego de grandes y esporádicas lluvias, mientras otras se reproducen sólo durante períodos intermitentes de pequeñas caídas de agua. Entre los anuros, aquellas especies que depositan los huevos en agua tienen un complemento ovárico más grande ($\bar{x}=1225$) que aquellas que depositan sus huevos en nidos de espuma en agua ($\bar{x}=457$) o en vegetación por encima del agua ($\bar{x}=342$). Especies que tienen huevos terrestres con desarrollo directo tienen huevos más grandes ($\bar{x}=2.72$ mm) que aquellas con huevos terrestres y con renacuajos ($\bar{x}=1.88$ mm). El factor tamaño del ovario (número de huevos $\times$ diámetro del huevo/longitud corporal de la hembra) es más grande en especies que depositan huevos en agua ($\bar{x}=24.7$) seguido por especies que depositan huevos en vegetación por encima del agua ($\bar{x}=8.9$) y en nidos de espuma ($\bar{x}=4.2$), y menor en aquellas especies que tienen huevos terrestres con desarrollo directo ($\bar{x}=1.2$). Hay una correlación positiva entre el número de huevos

y el tamaño de la hembra, dentro de un determinado modo reproductivo. En algunas especies hay una correlación positiva entre el tamaño de los huevos y el tamaño de las hembras, dentro de un determinado modo reproductivo.

Once modos reproductivos pueden separarse entre los anuros de Santa Cecilia:

1. Huevos depositados en amplios cuerpos de agua, con desarrollo de renacuajos en el agua. Las agrupaciones de huevos son grandes; huevos y recién nacidos son pequeños (35 especies).

2. Huevos y larvas con desarrollo en huecos de árboles llenos de agua. Las agrupaciones de huevos son moderadas en tamaño; huevos y recién nacidos son pequeños (*Nyctimantis rugiceps*).

3. Huevos depositados en nidos con forma de tazón. Agrupaciones de huevos grandes; los huevos y recién nacidos son pequeños (*Hyla boans*).

4. Huevos depositados en la vegetación por encima de aguas lénticas. Agrupaciones de huevos son moderadamente pequeñas; huevos son sólo ligeramente mayores que aquellos depositados en agua, y los pequeños recién nacidos caen al agua para completar su desarrollo (11 hylidos).

5. Huevos depositados en la vegetación por encima de aguas lólicas. Agrupaciones son pequeñas; huevos y recién nacidos son moderadamente grandes, y los recién nacidos caen al arroyo (3 *Centrolenella*).

6. Huevos suspendidos en un nido de espuma sobre el agua. Agrupaciones de huevos son moderadamente grandes; huevos y recién nacidos son pequeños (9 leptodactylinos).

7. Huevos depositados sobre el suelo; renacuajos recién nacidos llevados al agua en la espalda de adultos. Agrupaciones de huevos son pequeñas; huevos y recién nacidos son relativamente grandes (6 dendrobátidos).

8. Huevos depositados en nidos de espuma sobre tierra. Las posturas son moderadamente pequeñas y los huevos

relativamente grandes; renacuajos completan su desarrollo dentro del nido de espuma (*Adenomera andreae*).

9. Huevos depositados en tierra y con desarrollo directo en pequeños sapos; sin renacuajos acuáticos. Posturas pequeñas pero con grandes huevos (17 eleutherodactylinos y *Syncope*).

10. Huevos depositados en la espalda de la hembra en el agua y tienen desarrollo directo. Posturas moderadamente pequeñas, con huevos grandes (*Pipa pipa*).

11. Huevos llevados sobre la espalda de hembras no acuáticas y teniendo desarrollo directo. Posturas pequeñas y huevos grandes (*Hemiphractus proboscideus*).

Las modificaciones del modo general de reproducción en lagos parecen estar todas en relación con el incremento de la sobrevivencia de los huevos y de las larvas. Esto es logrado a través de numerosas y pequeñas posturas, remoción de huevos y/o larvas del agua, incremento del tamaño de los recién nacidos, o a través de cuidado parental. El incremento de la especialización reproductiva resulta en una reducción de la fecundidad pero en una mayor sobrevivencia. Generalistas, en sentido reproductivo, con alta fecundidad están mejor adaptados a ambientes no-predecibles.

Entre los lagartos, hay 13 especies que parecen tener reproducción continua, y siete discontinua; se desconoce la situación para las nueve restantes especies. Generalmente aquellas especies con reproducción continua son pequeñas (longitud corporal de hembras gravidas 26-100 mm); en cambio las de reproducción discontinua son un poco más grandes (longitud corporal 48-115 mm). Sólo *Mabuya mabouya* es vivípara. Aquellas de reproducción continua tienen múltiples posturas por año, mientras que aquellas de reproducción discontinua tienen sólo una postura por año.

Dos grandes clases de estrategias reproductivas existen entre los lagartos. Aquella con una madurez más temprana

y múltiples posturas se encuentra mayoritariamente en lagartos de posturas pequeñas. El tamaño de la postura puede ser un reflejo del tamaño del lagarto (microteiididos), capacidad de soporte de las lamelas adhesivas (geckónidos y *Anolis*), o la necesidad de un rápido escape (*Enyaliodes cofanorum* y *Plica umbra*). Tamaños grandes y movimientos lentos permiten posturas mayores en *Enyaliodes laticeps*, *Polychrus marmoratus* y *Kentropyx pelviceps*. La otra estrategia, con una madurez tardía y posturas únicas, se da en *Ameiva ameiva* y *Mabuya mabouya*.

Los patrones de reproducción no son evidentes en culebras, con los datos recogidos al menos. La escasez de hembras preñadas sugiere que la reproducción intraindividual puede ser anual o bianual. Las culebras vivíparas (8 especies) tienen nidadas más grandes ($\bar{x}=25.2$) que las 45 especies ovíparas ($\bar{x}=7.6$). Las delgadas serpientes arboreales (*Dipsas*, *Imantodes*, *Leptodeira*, *Leptophis*, y *Oxybelis*) no tienen más de seis huevos. Quizás estas serpientes se reproducen más frecuentemente que aquellas ovíparas de cuerpos pesados o que las vivíparas.

Bajo el régimen climático sin estaciones de Santa Cecilia la reproducción en la mayoría de las especies es acíclica. Hay una continua infusión de jóvenes en la población y generaciones superpuestas. La continuidad de reproducción tiende a disminuir la fluctuación poblacional y la tasa de extinción. Por ello, la erianza continua puede ser una de las razones de la alta riqueza en especies en las selvas húmedas del trópico.

En comparación con especies de ambientes estacionales, la mayoría de los anfibios y reptiles de las selvas lluviosas del trópico emplean muchas más estrategias reproductivas, se reproducen más frecuentemente, maduran más temprano, tienen un más alto potencial reproductivo por unidad de tiempo, y tienen poblaciones más estables, pero tienen más baja sobrevivencia y una corta vida.

El estudio de la estructura de la comunidad consistió primariamente en un análisis de la distribución del hábitat, de la actividad diaria, y de dieta y alimentación. Información en relación a los renacuajos, los cantos nupciales de los anuros, y relaciones entre los tamaños de las especies también fueron utilizados. La comunidad puede ser dividida en varios componentes: 1) diurnos y terrestres, 2) diurnos y arbóreos, 3) nocturnos y terrestres, 4) nocturnos y arbóreos, y 5) acuáticos. Análisis del sobremontaje de nichos de cada uno de los componentes revela una amplia superposición para varios recursos entre determinados tipos adaptativos y determinados niveles tróficos. En la determinación del número de especies que pueden coexistir en Santa Cecilia, lo siguiente fue considerado: 1) el espectro y abundancia de recursos disponibles, 2) la estabilidad de los recursos, 3) la extensión de la utilización del recurso por los miembros de la comunidad, y 4) la cantidad de sobremontaje en la utilización del recurso por los miembros de la comunidad.

El examen de estos criterios revela que en Santa Cecilia hay una alta diversidad abundancia de recursos disponibles y que el amplio sobremontaje en la de estos recursos indica que la competencia interespecífica no es importante para la regulación de las especies y sus tamaños poblacionales. Por el contrario, se postula que las poblaciones (especialmente aquellas de tipo *r*) están limitadas por la predación fluctuaciones aperiodicas del ambiente.

La comunidad herpetológica no está estructurada como las comunidades de aves. Las aves tienen especializaciones para dietas restringidas, diferentes estrategias para la persecución o búsqueda del alimento, y complejas interacciones sociales intraespecíficas e interespecíficas. En contraste, la mayoría de los anfibios y reptiles (especialmente sapos y lagartos) son generalistas con escaso o nulo comportamiento social. Por ello, no es sorprendente que muchos modelos

ecológicos que han tenido su origen conceptual en evidencias ornitológicas parecieran no aplicar a la comunidad herpetológica tropical.

En comparación con las comunidades herpetológicas de ambientes estacionales, las comunidades de las selvas tropicales sin demarcaciones estacionales gozan de un mayor espectro de recursos y una mayor dimensionalidad. Estas diferencias por sí solas pueden explicar la mayor riqueza en especies que hay en las comunidades tropicales.

Ocho patrones de distribución son evidentes entre las especies que componen la herpetofauna de Santa Cecilia. Cuatro de estos patrones incluyen a la totalidad de la cuenca amazónica; 28 anfibios y 56 reptiles (45% del total) caen dentro de estos cuatro patrones. Los otros cuatro patrones se reducen al alto Amazonas; son exhibidos por 66 anfibios y 35 reptiles (55% del total). Al comparar la herpetofauna de Santa Cecilia con aquellas de Iquitos, Perú; de Belém, Brasil; y de la Isla Barro Colorado, Panamá, se encuentra un alto grado de parecido faunístico entre Santa Cecilia e Iquitos y uno menor entre Santa Cecilia y Barro Colorado.

Sudamérica se separó de África cerca de 90 y de Australia cerca de 38 millones de años atrás. Durante la mayor parte del Terciario el continente se movió en un arco hacia Norteamérica, y una conexión de tierra continua entre Centroamérica y Sudamérica se formó aproximadamente 5.7 millones de años atrás. Aún cuando algún intercambio faunístico ocurrió entre Norte y Sudamérica a través de un archipiélago, Sudamérica estuvo efectivamente aislada de otros continentes en la mayoría del Terciario. Durante este tiempo, miembros de la mayoría de las familias de los anfibios y reptiles evolucionaron en Sudamérica. De los 25 grupos familiares de Santa Cecilia, 16 son de origen gondwanalándico; nueve otros invadieron Sudamérica desde Norteamérica—cuatro previo al Plógeno vía archipiélago y cinco luego del

establecimiento de la conexión de los continentes en el Plioceno. Se asume que al final del Plioceno (1.8 millones de años atrás) todas las familias y la mayoría, sino todos, de los géneros de anfibios y reptiles ahora conocidos en Santa Cecilia existían ya en Sudamérica en o alrededor de la cuenca amazónica.

La biota de la cuenca amazónica durante el Terciario y el Cuaternario estuvo influenciada por un lago que se retiraba gradualmente en la cuenca y por el levantamiento de los Andes. La selva pluviosa se dispersó sobre la tierra emergente pero a causa de la fluctuación entre períodos secos y húmedas del clima se tuvo contracciones periódicas de la selva lluviosa; las más recientes fases áridas ocurren hace 11.000 y 2500-4000 años atrás. Durante estas fases áridas la selva pluviosa persistió en refugios aislados; uno de los más grandes (Refugio Napo) abarcaba a Santa Cecilia. Las especies animales que habitan la selva lluviosa sobrevivieron en los refugios forestales y allí se diferenciaron. Si su diferenciación resultó en aislamiento reproductivo de otras poblaciones aisladas, la subsecuente reunificación de la selva

permitió a las recientemente formadas especies vivir en parapatría si ellas competían por recursos limitados, o en simpatría si los recursos necesarios no eran restringidos. Recursos abundantes permitieron la acumulación de la inmensa comunidad herpetológica en Santa Cecilia.

El presente trabajo es sólo una introducción al estudio de comunidades herpetológicas tropicales. Más estudios cuantitativos e intensos son necesarios. Estudios detallados sobre los ciclos reproductivos y sobre la frecuencia de los cruzamientos individuales son requeridos urgentemente. Desgraciadamente el hombre está destruyendo gradualmente la biota amazónica. Se requiere en forma urgente coleccionar series adecuadas de especímenes para estudios taxonómicos y distribucionales de la biota, pero esta clase de colecta compensatorio no permitirá estudiar las comunidades. Si se quiere tener un entendimiento de las comunidades de las selvas lluviosas tropicales en la cuenca amazónica es necesario establecer grandes reservas naturales que provean sitios de estudios y preservación de esta rica biota para la humanidad.

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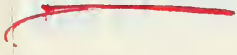
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